

1 **Phylogeny, disparity, and mass extinction response in the trilobite order Harpetida**

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7

8 **Abstract:** The trilobite order Harpetida has long been easily recognized but many  
9 unanswered evolutionary questions about the group remain. This work explores the  
10 phylogenetic relationships within Harpetida and studies the harpetid response to the Late  
11 Ordovician mass extinction to better understand the relationship between extinction  
12 events and disparity. A discrete morphological character matrix was assembled from  
13 published descriptions and refined through first-hand observations. This matrix is the first  
14 attempt of its kind to characterize the overall morphology of Harpetida, rather than  
15 focusing on individual harpetid genera. Phylogenetic analyses under both maximum  
16 parsimony and Bayesian inference optimality criteria retrieve tree topologies that support  
17 harpetid monophyly but throw doubt onto previous hypotheses of the internal  
18 relationships of the order. Harpetid disparity proves remarkably stable over time. A  
19 modest peak in the Ordovician is followed by a slow decline throughout the Silurian and  
20 Devonian. After the Ordovician period, harpetids demonstrate little or no ability to  
21 colonize new areas of morphospace. This may represent a fundamental failure to recover,  
22 where the lasting impacts of Late Ordovician mass extinction continue to suppress

23 morphological innovation. These findings demonstrate that mass extinction events may  
24 have complex impacts that play out over many millions of years.

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26

27 **Key words:** mass extinction, disparity, end-Ordovician extinction, morphospace,

28 phylogeny, trilobites

29 THE Late Ordovician (end-Hirnantian) mass extinction was the first of the five major  
30 extinction events to shape the evolutionary history of the Phanerozoic (Raup and  
31 Sepkoski 1982) and was responsible for eliminating an estimated 85% of marine species  
32 (Sheehan 2001). Of these five mass extinctions, the Late Ordovician event was the  
33 second most severe in terms of proportion of genera and families that disappeared  
34 (Sepkoski 1996). This mass extinction is generally attributed to a brief period of intense  
35 glaciation at the South Pole, and is thought to have occurred in two discrete pulses  
36 (Congreve 2013a; Harper *et al.* 2014). The first of these is ascribed to a sudden  
37 temperature decrease, and the second to the retreating of the ice sheets and the  
38 displacement of anoxic waters onto continental shelf habitats (Sheehan 1973; Sheehan  
39 2001; Brenchley *et al.* 2003; Congreve 2008; Finnegan *et al.* 2011; Scalfani *et al.* 2019).

40 Whether the Late Ordovician mass extinction had a substantial, long term impact  
41 on the subsequent evolution of biota has been called into question (Droser *et al.* 2000;  
42 McGhee *et al.* 2004; McGhee *et al.* 2012). In particular, McGhee *et al.* (2004) stated that  
43 the extinction failed to eliminate any ecologically dominant taxa or evolutionary  
44 innovations and was of minimal ecological impact. However, recent work (Congreve *et*  
45 *al.* 2019; Scalfani *et al.* 2019) has challenged this scenario, suggesting that many groups  
46 that survived the Late Ordovician mass extinction in fact experienced significant changes  
47 in their morphologies, which influenced their potential for subsequent evolutionary  
48 success. We address this issue by exploring whether the trilobite order Harpetida  
49 experienced major morphological changes following the Late Ordovician mass  
50 extinction.

51 Mass extinction events are responsible for macroecological turnovers and,  
52 ultimately, impose constraints on the long-term evolutionary success of clades (Harper *et*  
53 *al.* 2014). While much work has explored the effects of these events on taxonomic  
54 diversity, their impact on morphological disparity remains poorly understood (e.g.  
55 Dommergues *et al.* 1996; Lupia 1999; Thorne *et al.* 2011; Bapst *et al.* 2012; Korn *et al.*  
56 2013; Ruta *et al.* 2013; Lamsdell and Selden 2017; Sclafani *et al.* 2019). Why do some  
57 extinction events remove morphologies at random, while others are highly selective  
58 (Raup 1992; Jablonski and Raup 1995; Jablonski 2001; Korn *et al.* 2013)? Why do some  
59 clades survive extinctions but fail to occupy new areas of morphospace (Thorne *et al.*  
60 2011), while others seem primed for morphological innovation (Bapst *et al.* 2012)?  
61 Addressing these questions is important for understanding the patterns of evolution and  
62 extinction in the fossil record and for predicting how modern ecosystems may respond to  
63 future mass extinctions (Dirzo *et al.* 2014).

64 Previous studies have suggested that trilobites in particular exhibited unique  
65 patterns of survivorship following the Late Ordovician mass extinction. Chatterton and  
66 Speyer (1989) focused primarily on trilobite developmental strategy during the Late  
67 Ordovician and demonstrated that species with planktonic larvae were more prone to  
68 extinction. Congreve and Lieberman (2011) showed that sphaerexochine trilobites, which  
69 are thought to have had benthic larvae, were largely unaffected by the Late Ordovician  
70 mass extinction. However, the closely related deiphonine trilobites seem to have been  
71 much more strongly affected by this event, despite having a similar developmental  
72 strategy, lifestyle, and distribution (Congreve 2013*b*), suggesting a more complex  
73 scenario may have been at work. Additionally, the Late Ordovician mass extinction

74 eliminated all trilobites with a presumed pelagic adult lifestyle (Chatterton and Speyer  
75 1989).

76 Cold-water adaptations are thought to have been key to the survival and recovery  
77 of various trilobites. This idea was examined in homalonotid trilobites by Congreve  
78 (2013a), who concluded that a cold-water-adapted lineage was driven to evolve into a  
79 warm-water-adapted lineage following the end-Ordovician mass extinction. Finnegan *et*  
80 *al.* (2012) found that the maximum palaeolatitude at which a genus had been previously  
81 sampled, a macroecological trait linked to thermal tolerance, strongly influenced  
82 extinction risk during the Late Ordovician; specifically, they observed an unexpectedly  
83 high extinction rate of low-paleolatitude genera. Finnegan *et al.* (2016) examined both  
84 biogeographic and bathymetric factors and found that the extinction event preferentially  
85 affected genera restricted to deeper waters or to relatively narrow palaeolatitudinal  
86 ranges. All of this seems indicative of a strong ecological component to the mass  
87 extinction event. At family level, Adrain *et al.* (1998) confirmed that extinction patterns  
88 in Late Ordovician trilobites were related to clade size; families that survive the mass  
89 extinction are more diverse than families that do not.

90 The present contribution examines the phylogeny and morphology of harpetid  
91 trilobites. Harpetida Whittington, 1959 was an order of trilobites first recorded 500  
92 million years ago during the Late Cambrian (Hughes 2007) and went extinct during the  
93 Late Devonian at the base of the Upper Kellwasser Event (McNamara *et al.* 2009).  
94 Harpetids are identified by the horseshoe-shaped “harpetid brim”; long genal  
95 prolongations (broader and flatter than typical genal spines); reduced eyes, often with  
96 strong ridges; a small pygidium; and an anteriorly narrowing glabella (Fortey and Owens

1997). Because harpetid trilobites are morphologically distinctive (Fig. 1, Fig. 2), they are an ideal group for the discovery of informative phylogenetic characters. In addition, harpetids were one of a handful of trilobite orders to survive the Late Ordovician mass extinction (Hughes 2007). As such, harpetids are also an ideal model group for exploring models of post-extinction recovery, specifically linking patterns of disparity change with fluctuations in taxic richness.

103

#### 104 **HISTORY OF THE HARPETIDA CONCEPT**

105 Harpetida was raised to ordinal status by Ebach and McNamara (2002). The  
106 group was previously placed within Ptychopariida, but harpetids are distinguished from  
107 true ptychopariids by their marginal facial sutures and lack of a rostral plate (Ebach and  
108 McNamara 2002). Ebach and McNamara (2002) recognized three harpetid families,  
109 Harpetidae, Harpididae, and Entomaspidae, and approximately 30 genera. Although the  
110 monophyly of the group is generally accepted, Adrain (2011) did not positively identify a  
111 unified Harpetida. Instead, he placed the family Harpetidae (including those species  
112 previously assigned to Entomaspidae) within the order Harpida, while regarding the  
113 family Harpididae as *incertae sedis*.

114 Drawing on the conclusions of Fortey and Owens (1999), Adrain *et al.* (2004)  
115 described members of the family Harpetidae as belonging to a morpho-functional group  
116 of small, filter-feeding trilobites, characterized by a vaulted cephalic chamber flanked by  
117 genal prolongations, a thorax suspended above the sediment surface, weak axial  
118 musculature, a hypostome held above the level of the cephalic margin, and (usually)  
119 reduced eyes. While highly generalized, this description offers a basis for understanding

120 the harpetid morphotype. Early work in experimental biomechanics (Pearson 2017) has  
121 suggested that other members of this morpho-functional group are unlikely to have been  
122 genuine filter feeders, casting uncertainty onto harpetids' ecological adaptations. Much of  
123 the debate hinges upon the function of the harpetid brim, which has been variously  
124 suggested to act as a plough, a sieve, a hydrostatic device, a sensory or respiratory organ,  
125 or a structure for strengthening and lightening the exoskeleton (Ebach and McNamara  
126 2002; McNamara et al. 2009).

127

## 128 **THE STUDY OF DISPARITY**

129 While taxonomic diversity measures the number of taxa within a clade, disparity,  
130 or morphological diversity, measures the range of forms (Foote 1991a; Foote 1992b;  
131 Foote 1993; Foote 1994; Wills *et al.* 1994; Foote 1995; Foote 1997; Roy and Foote  
132 1997). There are essentially two ways to quantify disparity (Briggs *et al.* 1992, Villier  
133 and Eble 2004; Hetherington *et al.* 2015; Deline *et al.* 2018). The first is through  
134 morphometrics, which can be further broken down into those techniques that use  
135 continuous measurements (traditional morphometrics) and those that use landmarks  
136 (geometric morphometrics). However, reliable morphometric data can be problematic to  
137 collect when working with taxa with highly variable or divergent morphologies. The  
138 alternative approach is to use discrete characters (which can be combined with  
139 continuous data), often derived from cladistic data (Foote 1992b; Wills *et al.* 1994;  
140 Wanger 1995; Lloyd 2016; Hopkins and Gerber 2017; Guillerme *et al.* 2020). Character-  
141 based disparity analyses overcome some of the challenges associated with divergent  
142 morphology and multiple comparative studies have used discrete characters successfully

143 to study shifts in disparity over time and across multiple mass extinctions (Foote 1994,  
144 1999; Wills 1998; Lofgren *et al.* 2003; Wesley-Hunt 2005; Young *et al.* 2010; Thorne *et*  
145 *al.* 2011; Bapst *et al.* 2012; Hughes *et al.* 2013; Ruta *et al.* 2013; Lamsdell and Selden  
146 2017).

147 Notably, character-based disparity analyses appear to yield findings comparable  
148 to more conventional, morphometric approaches (Villier and Eble 2004; Hetherington *et*  
149 *al.* 2015). Hetherington *et al.* (2015), looking at caecilian amphibians, found that  
150 disparity measurements based on skull morphometrics correlated well with disparity  
151 measurements based on discrete neuroanatomical characters. This supports the earlier  
152 findings of Villier and Eble (2004), saw patterns of high early disparity in both landmark  
153 and character-based analyses of spatangoid echinoids. However, assessments of disparity  
154 from traditional morphometrics may diverge from the other methods when very different  
155 aspects of morphology are being measured; Villier and Eble (2004) cite the example of  
156 quantifying an echinoid's overall shape, as opposed to its tuberculation and plate  
157 architecture.

158 Brusatte *et al.* (2011) built on the idea of character-based disparity and presented  
159 a method for phylogenetically correcting for missing data in such studies. The method  
160 infers hypothetical ancestors at every node of the phylogenetic tree, reconstructs their  
161 character states, and includes them in the disparity analysis as if they were sampled taxa.  
162 Halliday and Goswami (2015) expanded on this approach by introducing the “extended  
163 punctuational” method, which gives reconstructed ancestors a temporal range, rather than  
164 having them appear only in a single time bin. This technique better enables direct  
165 comparisons between disparity measures and taxonomic diversity measures, which are

166 often phylogenetically corrected, and is especially useful for groups with periods of low  
167 sampled diversity, such as harpetids. However, this method must be applied cautiously,  
168 as the reconstructed ancestors are not truly independent data points and may introduce  
169 problematic side effects (e.g. smoothing bias) (Lloyd 2016; Guillerme et al. 2020).

170         Using a wide variety of approaches to study disparity, Foote (1997) concluded  
171 that the evolution of morphological disparity is typically non-uniform, often expanding  
172 early in clade history while taxonomic diversity remains comparatively low. Hughes *et*  
173 *al.* (2013) likewise found that clades tend to reach their highest morphological disparity  
174 early in their evolutionary history. However, this pattern can be truncated by mass  
175 extinction events (Hughes *et al.* 2013), which is consistent with findings suggesting that a  
176 wide variety of environmental factors contribute to patterns of disparity, including global  
177 sea level (Dommerrgues *et al.* 1996), bathymetry (McClain 2005; Hopkins 2014),  
178 substrate (Hopkins 2014), temperature (Hopkins 2014), and salinity (Lamsdell and  
179 Selden 2017).

180         Whatever the contributing factors, it has long been recognized that taxonomic  
181 diversity and disparity are frequently decoupled (Foote 1993; Lupia 1999; Thorne *et al.*  
182 2011; Hopkins 2013; Ruta *et al.* 2013; Congreve *et al.* 2018). Hopkins (2013) studied this  
183 phenomenon in Cambrian trilobites and concluded that signals of high disparity with low  
184 taxonomic diversity are more likely the results of random or mean-targeted extinction,  
185 rather than increased rates of morphological diversification. This finding is of particular  
186 relevance to this study, given its focus on the harpetid response to mass extinction.

187

188 **DISPARITY AND MASS EXTINCTION**

189           Mass extinctions can impact disparity in various ways. Korn *et al.* (2013),  
190 studying the Devonian and Permian extinction events, suggested that disparity could be  
191 affected during periods of widespread extinction in accordance with one of three general  
192 modes. The first mode is essentially random, where available morphologies are removed  
193 in a nonselective fashion. In this mode, overall morphospace occupation is not affected.  
194 Possible examples of this are seen in ammonoids during the Toarcian–Aalenian transition  
195 (Simon *et al.* 2010) and end-Permian mass extinction (Korn *et al.* 2013), and in blastoid  
196 echinoderms (Foote 1991b). The second characteristic mode is marginal, where the edges  
197 of morphospace are selectively and symmetrical trimmed. In this mode, overall variation  
198 is reduced. Possible examples of this are seen in phacopid and proetid trilobites (Foote  
199 1993). Finally, the mode of extinction may be lateral, with asymmetric selection  
200 eliminating a particular region of previously occupied morphospace. In this mode, the  
201 centroid of occupied morphospace shifts position. Possible examples of this are seen in  
202 the response of ammonoids to the Kellwasser and Hangenberg events (Korn *et al.* 2013).

203           Additionally, Lamsdell and Selden (2017) examined the disparity of eurypterids  
204 and suggested that even when mass extinctions remove morphologies with a high degree  
205 of apparent randomness, recovery (i.e. re-expansion following a morphological  
206 bottleneck) is often limited to those taxa that share a limited range of morphologies. This  
207 finding is consistent with the work of Thorne *et al.* (2011), Congreve *et al.* (2018), and  
208 Sclafani *et al.* (2019).

209           The disparity of phylogenetic groups tends to decrease over time, particularly  
210 during the interval immediately before or after a mass extinction (Zelditch *et al.* 2003).  
211 Valentine (1995) suggested that this may be due to a decrease in available ecological

212 habitats, while Gould (1991) suggested it may result from an increase in developmental  
213 constraints. Crônier expanded on this idea of developmental constraint in her work on  
214 phacopid trilobites (Crônier and Courville 2003; Crônier *et al.* 2005, 2011; Crônier and  
215 Fortey 2006; Crônier 2007, 2010, 2013). Her findings demonstrated that changes in the  
216 timing of development (i.e. heterochrony) were an important source of disparity in  
217 trilobites. In times of ecological stress, such as sea level rise, trilobites tended to revert to  
218 more juvenile (paedomorphic), presumably less specialized forms (Crônier 2013). This  
219 reduced overall disparity by encouraging generalist morphologies.

220         Extinction events can also have a variety secondary or indirect effects on disparity  
221 and diversity. These can include adaptive radiations (Sunberg 1996; Bapst *et al.* 2012),  
222 where disparity and diversity both increase rapidly after a period of sharp decrease.  
223 Alternatively, disparity may fail to recover despite modest gains in diversity (Thorne *et*  
224 *al.* 2011; Ruta *et al.* 2013).

225         To understand the various responses to mass extinctions, further case studies are  
226 needed. No previous study has explicitly explored the disparity of Harpetida and many  
227 fundamental questions about harpetid morphology and phylogeny remain unanswered  
228 (Ebach and McNamara 2002). Moreover, the question of selectivity in the Late  
229 Ordovician mass extinction remains open (Adrain *et al.* 1998; McGhee *et al.* 2004;  
230 Finnegan *et al.* 2012, 2016; Sclafani *et al.* 2019), especially with regard to trilobites  
231 (Chatterton and Speyer 1989; Congreve and Lieberman 2011; Congreve 2013*a, b*). In  
232 using harpetid disparity to explore selectivity during the Late Ordovician mass extinction,  
233 this work seeks to shed light on both of these issues.

234

235 **METHODS**

236 *Phylogenetic Methods*

237 We summarized harpetid morphology in the form of a discrete character matrix  
238 (Supplemental Table 1), drawing upon the published trilobite literature. We drew many  
239 characters in this matrix from the *Treatise on Invertebrate Paleontology* (Fortey and  
240 Owens 1997) and from Ebach and McNamara (2002), which was a review of harpetid  
241 systematics that presented a number of discrete morphological characters (between 3 and  
242 26 for each genus, exclusively concerning the cephalon and related structures) that were  
243 incorporated into several genus-level character matrices. Our study elevated this work to  
244 the ordinal level by synthesizing the relevant characters from these genus-level matrices  
245 together with characters drawn from the *Treatise* and direct observations of specimens  
246 housed at the Yale Peabody Museum of Natural History.

247 We coded 76 discrete morphological characters (Appendix 1; Supplemental Figure 1; [the](#)  
248 [data matrix is also available in the online MorphoBank database \[O’Leary and Kaufman](#)  
249 [2012\] under the project code p2804, accessible at](#)  
250 <http://morphobank.org/permalink/?P2804>), including 69 cephalic characters, three  
251 thoracic characters, and four pygidial characters. We included data coded from 47  
252 species, using 35 museum specimens observed firsthand, 14 museum specimens observed  
253 digitally, and c. 160 published figures. The coded taxa included 21 of the 29 recognized  
254 harpetid genera, and included multiple representatives of each of the three previously  
255 recognized harpetid families: Entomaspididae, Harpididae, and Harpetidae. The  
256 remaining 8 genera, *Chencunia* Qiu, 1984; *Kathrynia* Westrop, 1986; *Palaeoharpes* Lu  
257 and Qian in Zhou *et al.*, 1977; *Dictyocephalites* Bergeron, 1895; *Kitatella* Petrunia in

258 Khalfin, 1960; *Metaharpides* Pillet and Courtessole, 1981; *Paraharpides* Pillet and  
259 Courtessole, 1981; and *Pscemiaspis* Abdullaev and Khaletskaya, 1970 were excluded due  
260 to the difficulty of procuring adequate fossil material or figures from which to code  
261 character states (Table 1); the harpidid genus *Chencunia*, for example, is currently known  
262 only from a few partial pygidia from the Upper Cambrian of China (Qiu 1984). Six  
263 ptychopariid trilobites were included as outgroup taxa, with the analysis rooted on a  
264 seventh outgroup, the redlichiid *Eoredlichia intermedia* Lu, 1940.

265         To test harpetid monophyly, we need to include several ptychopariids in our data  
266 matrix, as it could not be known which ptychopariid taxa would prove most closely  
267 related to Harpetida. Lamsdell and Selden (2014) included both ptychopariids and  
268 harpetids in a data matrix designed to robustly test the monophyly of proetid trilobites.  
269 The work suggested several ptychopariid genera as viable candidates for inclusion in our  
270 new matrix, including *Modocia*, *Coosella*, *Crepicephalus*, and *Tricrepicephalus*. These  
271 four taxa represent a broad sampling of Ptychopariida, capturing much of the disparity of  
272 the group. In addition, we chose to include representatives of the ptychopariid genera  
273 *Cedaria* and *Ptychoparia*. The similarity between these trilobites and the members of  
274 Harpetida has been noted by Rasetti (1945) in his work on the more basal members of the  
275 order (i.e. the entomaspidids). The notion of including a trinucleid trilobite (order  
276 Asaphida) was considered and eventually discarded on the basis of the high degree of  
277 morphological convergence currently assumed between trinucleid and harpetid trilobites  
278 (Adrain *et al.* 2004). To provide structure, the outgroup was rooted on *Eoredlichia*  
279 *intermedia*, from the paraphyletic order Redlichiida, thought to be the group that gave  
280 rise to Ptychopariida during the Early to Middle Cambrian (Hughes 2007).

281 We performed parsimony analysis in TNT (Tree analysis using New  
282 Technology) (Goloboff *et al.* 2008). The data matrix was subjected to cladistic analysis,  
283 employing random addition sequences followed by tree bisection–reconnection (TBR)  
284 branch swapping with 100,000 repetitions with all characters unordered and of equal  
285 weight; for more on the subject of differential character weighting see Congreve and  
286 Lamsdell (2016). We also conducted Bayesian inference analyses in MrBayes 3.2.6  
287 (Huelsenbeck and Ronquist 2001) with four independent runs of 100,000,000 generations  
288 and four chains each under the maximum likelihood model for discrete morphological  
289 character data (Mkv +  $\Gamma$ : Lewis 2001), with gamma-distributed rate variation among  
290 sites. All characters were treated as unordered and equally weighted (Congreve and  
291 Lamsdell 2016). Trees were sampled with a frequency of every 100 generations, resulting  
292 in 1,000,000 trees per run. The first 25,000,000 generations (250,000 sampled trees) of  
293 each run were discarded as burn-in, and the 50% majority rule consensus tree calculated  
294 from the remaining 750,000 sampled trees across all four runs. Posterior probabilities  
295 were calculated from the frequency at which a clade occurred among the sampled trees  
296 included in the consensus tree.

### 297 *Disparity Methods*

298 The disparity analysis relied on scripts written in R, adapted from the work of  
299 Hughes *et al.* (2013). Discrete morphological characters from the character matrix were  
300 converted to generalized pairwise Euclidean distances (GED). These distances differ  
301 from the other most commonly used distance metric, Gower’s coefficient (GC) (Gower  
302 1971), primarily in the ways they handle missing data. The GED metric inserts a  
303 weighted mean fractional univariate distance based on those distances that are calculable,

304 while the GC metric simply rescales calculable distances based on the amount of  
305 information available. Our GED distances were then combined with the known age  
306 ranges of harpetid taxa to track changes in disparity over geological time. Disparity was  
307 quantified based on the sums of ranges (measuring amount of morphospace occupied)  
308 and of variances (measuring dispersion of taxa around group centroids) (Foote 1992a;  
309 Wills *et al.* 1994; Ruta *et al.* 2013). We binned taxa from the matrix by geological age  
310 and produced morphospace plots, each representing the suite of available morphologies at  
311 a different point in the history of Harpetida. Multivariate statistical tests (PERMANOVA  
312 – permutational multivariate analysis of variance using the Euclidean distance measure)  
313 were performed in the software package PAST (Hammer *et al.* 2001) to test the  
314 significance of overlap and separation of groups of taxa across all axes between time bins  
315 at the period, stage, and epoch levels (Anderson 2017). Significance was estimated by  
316 permutation and resampling of the taxa across groups with 9999 replicates. Statistical  
317 analysis was performed with and without Bonferroni correction to control the familywise  
318 error rate (Dunn 1961; Armstrong 2014). Particular attention was devoted to changes  
319 across the Late Ordovician mass extinction boundary. Bonferroni corrections have been  
320 criticized as overly conservative (Sokal and Rohlf 1995; Moran 2003; Nakagawa 2004;  
321 Garamszegi 2006) but for this study we found it appropriate to skew against false  
322 positives.

323         We inferred the habitat affinities of harpetid genera by adapting the methods of  
324 Kiessling and Aberhan (2007). Harpetid occurrence data were taken from the  
325 Paleobiology Database. For a few recently described genera (*Eskoharpes*, *Globoharpes*,  
326 *Notchpeakia*) occurrence data were instead taken from the primary literature. We chose

327 to classify occurrences either deep water (deep subtidal to abyssal) or shallow water  
328 (marginal marine to shallow subtidal, including reefs) based on the reported depositional  
329 environments. The apparent affinity of each genus ( $A_g$ ) was calculated as

$$330 \quad A_g = \frac{g_h}{Total_h} / \frac{g_i}{Total_i}$$

331 where  $g_h$  was the number occurrences of genus  $g$  in habitat  $h$ ,  $g_i$  was the number of  
332 occurrences of genus  $g$  in habitat  $i$ ,  $Total_h$  was the total number of PBDB collections over  
333 genus  $g$ 's stratigraphic range collected from habitat  $h$ , and  $Total_i$  was the total number of  
334 PBDB collections over genus  $g$ 's stratigraphic range collected from habitat  $i$ . An  $A_g$   
335 greater than one indicates an apparent affinity for habitat  $h$ , while an  $A_g$  less than one  
336 indicates an apparent affinity for habitat  $i$ . Whether  $A_g$  is significant was determined by  
337 an exact one-sided binomial test (Kiessling and Aberhan 2007). As the absence of strictly  
338 significant affinities is primarily due to low sample sizes, we assigned affinities based on  
339 marginal significance ( $p \leq 0.1$ ) (Kiessling and Aberhan 2007). Taxa that could have  
340 reached marginal significance given their abundance, but whose actual probability of  
341 having an affinity for a particular habitat was not significant were classified as  
342 generalists. PERMANOVA testing was used determine whether harpetids with differing  
343 habitat affinities occupied significantly different areas of morphospace.

344 Additionally, PERMANOVA tests were used to verify that harpetids belonging to  
345 different taxonomic families occupied significantly different areas of morphospace. This  
346 method explored the possibility of correlation between harpetid distribution in  
347 morphospace and phylogenetic clade membership.

348 We included reconstructed ancestors in addition to the sampled taxa to  
349 phylogenetically correct for intervals of low sampling. We generated these according the

350 methods described by Brusatte *et al.* (2011) and Halliday and Goswami (2015). We  
351 mapped reconstructed characters onto the nodes of the parsimony consensus tree using  
352 Mesquite (Maddison and Maddison 2018) and coded each node as if it were a sampled  
353 taxon. Thirty-six reconstructed harpetids were generated in all. These reconstructed taxa  
354 were assigned age ranges using the “extended punctuational” method (Halliday and  
355 Goswami 2015). This method treats the ancestral morphology as occurring along the  
356 entire phylogenetic branch so that the total morphological disparity of each time bin can  
357 be accurately assessed (Halliday and Goswami 2015).

358

## 359 **RESULTS**

### 360 *Phylogenetic Analysis*

361 The parsimony analysis yielded 18 most parsimonious trees with an ensemble  
362 Consistency Index of 0.456, an ensemble Retention Index of 0.815, a Rescaled  
363 Consistency Index of 0.572, and a tree length of 189. A strict consensus of these trees is  
364 shown in Figure 3. Bayesian inference analysis retrieved a broadly similar set of  
365 relationships, also shown in Figure 3. The parsimony strict consensus tree showed a  
366 monophyletic Harpetida preceded by a paraphyletic grade of ptychopariid trilobites. In  
367 the Bayesian analysis *Ptychoparia striata* appeared as the sister to group to Harpetida  
368 (Fig. 3).

369 Two of the three previously recognized harpetid families—Harpetidae and  
370 Harpididae—were retrieved as monophyletic groups in both Bayesian and parsimony  
371 analyses. By contrast, Entomaspidae consistently appeared as a polyphyletic grade of  
372 basal harpetids, with Harpididae clustered within Entomaspidae. The entomaspidid

373 *Baikadimapsis jikdongensis* appeared as the sister to all other harpetids in both Bayesian  
374 and parsimony analyses.

375 Three taxa previously assigned to Harpetidae (*Conococheaguea ovata*, *Bowmania*  
376 *lassieae*, and *Heterocaryon vargum*) also fell within the entomaspidid grade. In both  
377 Bayesian and parsimony analyses, these three taxa formed a clade within the  
378 entomaspidid grade, which may indicate support for a monophyletic Heterocaryonidae.

379 The remaining harpetidids formed a large clade. This group included  
380 representatives of many recognized harpetid genera. Of these, *Eoharpes*, *Dubhglasina*,  
381 *Brachyhipposiderus*, *Bohemoharpes*, *Kielania*, *Globoharpes*, *Eskoharpes*, and  
382 *Dolichoharpes* appeared as monophyletic in both Bayesian and parsimony analyses. In  
383 the parsimony analysis *Hibbertia* appeared as a paraphyletic grade, while *Scotoharpes*  
384 was found to be polyphyletic. Bayesian analysis retrieved a monophyletic *Hibbertia* but a  
385 paraphyletic *Scotoharpes*. Both analyses found *Lioharpes* to be polyphyletic and *Harpes*  
386 to be either polyphyletic or paraphyletic. Collectively this group corresponded well with  
387 the established harpetid family Harpetidae and is defined by a wide bilamellar brim,  
388 marginal sutures, and small, tuberculate eyes. The entomaspidid trilobite *Entomaspis*  
389 *radiatus* was retrieved as the sister group to Harpetidae in both analyses.

#### 390 *Disparity Analysis*

391 Disparity levels remained largely stable within Harpetida over time. Analyses at  
392 the stage and epoch level failed to show statistically significant changes in the sum of  
393 variances over time (Fig. 4), but analysis at the period level suggested that harpetid  
394 disparity reached a modest maximum in the Ordovician and then declined steadily until  
395 the group's extinction in the Late Devonian (Fig. 5). At all levels of analysis, the sum of

396 ranges likewise showed a slow overall decline following a modest peak in the Ordovician  
397 (Fig. 4; Fig. 5).

398 Harpetid morphospace occupation remained statistically significantly different for  
399 all four time periods (Table 2; Fig. 6). From their initial occupied region of morphospace,  
400 early harpetids initially expanded their overall morphospace occupation as the group  
401 diversified and then underwent a migration in occupied morphospace via a vacation  
402 through extinction of their ancestral morphospace region and preferential radiation within  
403 the newly occupied area of morphospace, so that from the Middle Ordovician onward  
404 morphospace occupation has largely inverted, with overall morphospace occupation  
405 decreasing on slightly as the group transitioned into the Silurian. Originations continue  
406 across this newly defined region of morphospace until the Late Devonian, where another  
407 shift occurs with the centroid migrated toward what had previously been the margins of  
408 occupied morphospace, again driven by preferential extinction within specific sub-  
409 regions of morphospace.

410 As expected, harpetid distribution in morphospace is largely correlated with  
411 phylogenetic clade membership. PERMANOVA testing of family level partitions showed  
412 highly significant statistical differences in the morphospace occupied by each putative  
413 harpetid family, with the lowest levels of significance seen between Entomaspidae and  
414 Harpididae (Table 3). The most populous family, Harpetidae, occupied a distinct region  
415 of morphospace encompassing about half of the total occupied morphospace, including  
416 the regions occupied in the Middle Ordovician and Late Devonian. Harpididae,  
417 Heterocaryonidae and entomaspids occupy overlapping regions of morphospace  
418 incorporating the regions occupied in the Cambrian and Early Ordovician (Fig. 7).

419 PERMANOVA testing showed that inferred shallow water harpetids occupied  
420 significantly different areas of morphospace than inferred deep water harpetids (Table 4).  
421 Shallow water taxa also occupied significantly different areas of morphospace than  
422 generalist taxa. However, generalist taxa did not occupy significantly different areas than  
423 deep water taxa (Table 4). Specifically, shallow water taxa occupy areas of harpetid  
424 morphospace including the Cambrian and Early Ordovician region as well as region  
425 colonized during the Middle Devonian. Deep water taxa are predominantly located in the  
426 region of morphospace occupied in the Late Devonian (Fig. 8).

427

## 428 **DISCUSSION**

### 429 *Harpetid Phylogeny*

430 *Harpetid Monophyly.* Both our Bayesian and parsimony trees show strong support for the  
431 monophyly of harpetids. They group separately from all of the varied ptychopariids  
432 included in the analysis, representing a unique order within the subclass Librostoma.

433 *Entomaspidid Polyphyly.* In the retrieved phylogenies, harpidids are nested within the  
434 polyphyletic entomaspidids. The harpidid clade includes all three of the harpidid taxa  
435 present in the data matrix and is defined by several morphological characters, such as a  
436 genal ridge running posterolaterally from the eye; concave genae; radiating,  
437 anastomosing genal caecae; an expanded L3; and the lack of genal spines. In addition,  
438 some (though not all) harpidids are distinguished by marginal sutures. Importantly, this  
439 suggests that the so-called “hypoparian” suture condition, where the cephalic sutures skirt  
440 the margin of the cephalon (Raw 1949), emerged at least twice within the harpetids: once  
441 in the harpidids and once again in the harpetidids. Given the number of morphological

442 characters uniting the recognized harpidids, it seems desirable to retain the family  
443 Harpididae, though the group currently falls within the entomaspidid grade.

444         Three taxa previously assigned to the harpetidids —*Conococheaguea ovata*,  
445 *Bowmania lassieae*, and *Heterocaryon vargum*—also form a small clade within the  
446 entomaspidid grade. That these three should resolve here, rather than among the  
447 harpetidids, is perhaps unsurprising given their unusual morphology. For example, none  
448 of these taxa displays the usual “harpetid brim” (Fig. 2). *Bowmania* instead sports a wide  
449 fringe of radiating spines (Ludvigsen 1982; Adrain and Westrop 2004) that may have  
450 performed a similar ecological function, making it perhaps the most morphologically  
451 unusual of all harpetids. Meanwhile *Conococheaguea* and *Heterocaryon* have no brim-  
452 equivalent structure, only a narrow trough (Rasetti 1959; Adrain and Westrop 2004).  
453 Moreover, these taxa lack other key harpetidid synapomorphies, such as a tuberculate eye  
454 structure, alae, marginal sutures, and broad, flattened genal prolongations.

455         The genera *Conococheaguea*, *Bowmania*, and *Heterocaryon* should be removed  
456 from the harpetidids and assigned to a separate family. *Heterocaryon* was once the type  
457 for the trilobite family Heterocaryonidae, proposed by Hupé (1953). The family is no  
458 longer recognized, due to the supposed similarity between the genera *Heterocaryon* and  
459 *Bowmania* and the genus *Entomaspis* in both cephalic and pygidial structure (Ludvigsen  
460 1982). However, these findings indicate that the name could be resurrected to describe  
461 this new clade of harpetids, which until this point have remained largely in a taxonomic  
462 limbo (Hupé 1953; Rasetti 1959; Jell and Adrain 2002). This new incarnation of the  
463 family Heterocaryonidae is defined by a few key synapomorphies, including high  
464 cephalon convexity and equilateral glabellar lateral margins.

465 *Harpetidid Genera*. With *Conococheaguea*, *Bowmania*, and *Heterocaryon* recognized as  
466 heterocaryonidids, the harpetidids resolve as a clade. They are the largest harpetid family  
467 and include many currently recognized genera. However, the monophyly of several of  
468 these genera now appears dubious.

469         The genus *Scotoharpes* is clearly polyphyletic. Most species of the putative genus  
470 form a loose grouping, with a clade of three taxa (“*Scotoharpes*” *spasski*, “*Scotoharpes*”  
471 *tatouyangensis*, and “*Scotoharpes*” *raaschi*) forming a polytomy with two other  
472 *Scotoharpes* species, as well as a substantial clade of other harpetidids. Yet even if these  
473 two *Scotoharpes* (“*Scotoharpes*” *loma* and *Scotoharpes* *domina*, the type species for the  
474 genus) group with the others, this grouping would be paraphyletic. There are also two  
475 other supposed *Scotoharpes* (“*Scotoharpes*” *latior* and “*Scotoharpes*” *consuetus*) that fall  
476 much more basally within the harpetidids and do not appear closely related to each other.  
477 Therefore, *Scotoharpes* monophyly is rejected.

478         Some characters that were supposedly diagnostic for *Scotoharpes*, such as a  
479 glabella that is longer than it is wide, deep posterior glabellar furrows, the absence of a  
480 large anterior boss, and the anterior-posterior position of the eyes (Ebach and McNamara  
481 2002), now appear plesiomorphic for harpetidids. Others, such as low alae, deep pits  
482 demarcating the outer margin of the genal roll, and a flat preglabellar field, appear in only  
483 some species of the genus. This finding supports the assessment of Ebach and McNamara  
484 (2002), who noted in passing that *Scotoharpes* might very well be non-monophyletic and  
485 consist of several clades, describing the genus as a “dumping ground”.

486         *Lioharpes* also appears to be polyphyletic. The two species in this analysis resolve  
487 in a polytomy in the parsimony consensus tree and resolve as polyphyletic in the

488 Bayesian tree. As with *Scotoharpes*, the members of *Lioharpes* seem to share a  
489 generalized harpetid morphology, with little to unite them in particular. For example, the  
490 radiating ridges found at the genal roll-brim boundary, thought by Fortey and Owens  
491 (1997) to be diagnostic for *Lioharpes*, are also seen in other harpetidid genera such as  
492 *Bohemoharpes* and *Scotoharpes* (Norford 1973; Ebach and McNamara 2002). Likewise,  
493 the narrow alae seen in *Lioharpes* are also seen in some *Scotoharpes*, *Dubhglasina*, and  
494 *Brachyhipposiderus*, suggesting this character is plesiomorphic for harpetidids (Norford  
495 1973; Ebach and McNamara 2002).

496         The genus *Helioharpes* has already been identified as a subjective synonym of  
497 *Harpes* by Jell and Adrain (2002). This study supports this conclusion; both  
498 ‘*Helioharpes*’ included in our analysis independently appear as sister taxa to separate  
499 clades of *Harpes*. In fact, recognizing the synonymy of *Harpes* and *Helioharpes* almost  
500 reveals a monophyletic *Harpes*, as all ‘*Helioharpes*’ and *Harpes* in this analysis form a  
501 single clade. However, this clade also contains the genus *Dolichoharpes*.

502         Several potential solutions exist. One is simply to synonymize *Dolichoharpes*  
503 with *Harpes*. This would create a monophyletic *Harpes*, but may seem unsatisfactory, as  
504 many *Dolichoharpes* have a distinctive appearance that is different from other harpetidids  
505 (Whittington 1949). In particular, the genal prolongations of *Dolichoharpes* often appear  
506 narrower than those of *Harpes*, sometimes dramatically so as in the case of  
507 *Dolichoharpes dentoni* (the representative of the genus included in this analysis; see Fig.  
508 1). However, this striking change in appearance is achieved by a relatively small angular  
509 rotation of the genal spines, and *Harpes* and *Dolichoharpes* are united by many other,  
510 subtler morphological similarities. For example, anterolaterally directed eye ridges

511 appear to be a synapomorphy of *Dolichoharpes* and *Harpes* (including ‘*Helioharpes*’)  
512 (Ebach and McNamara 2002). Therefore, it may be best to treat *Dolichoharpes* in  
513 synonymy with *Harpes*, or to acknowledge that *Harpes* may comprise multiple  
514 recognizable genera. Complicating the issue is that fact that *Harpes* is another  
515 phylogenetic “dumping ground” (Ebach and McNamara 2002) for ambiguous harpetid  
516 taxa. As such, *Harpes* (as presently conceived) may well be genuinely polyphyletic,  
517 consisting of two related but distinct clades, each also closely related to *Dolichoharpes*.  
518 In this case, the clade containing the type species, *Harpes macrocephalus*, would be the  
519 genuine *Harpes*, while the other may represent a novel genus.

520         Another possible instance of paraphyly is seen in *Hibbertia*. The two *Hibbertia*  
521 included in this study appear in the parsimony consensus tree as a grade leading to the  
522 problematic *Harpes* and/or *Dolichoharpes* clade discussed above. However, in the  
523 Bayesian tree *Hibbertia* resolves as a clade. Further research is needed to fully assess the  
524 monophyly of this genus.

525         All other harpetidid genera included in this analysis appear to form monophyletic  
526 groups. Some of these are represented by only one species, and so their monophyly has  
527 yet to be genuinely tested; such is the case for *Kielania*, *Brachyhipposiderus*, and  
528 *Dubhglasina*. Other genera, such as *Globoharpes* and *Eskoharpes*, appear well supported.  
529 *Eskoharpes* is particularly notable, as its clade includes “*Harpes*” *neogracilis*, supporting  
530 its transfer to *Eskoharpes* by McNamara *et al.* (2009).

### 531 *Disparity in Harpetida*

532 *Disparity Through Time*. In the disparity corrected analysis, the sum of ranges and sum of  
533 variance (Fig. 4; Fig. 5) both show only a muted peak in harpetid disparity during the

534 Ordovician. If genuine, this early peak may represent the initial diversification of  
535 harpetids, which would be consistent with the work of previous researchers (Foote 1997;  
536 Hughes *et al.* 2013) who found that clades generally morphologically diversify early in  
537 their history.

538         No abrupt Late Ordovician decline is seen in harpetid disparity (Fig. 4; Fig. 5).  
539 Instead, disparity appears to decrease slowly and steadily from the Late Ordovician  
540 onward. The rate of decrease does not significantly increase during the Late Ordovician  
541 mass extinction. This finding closely resembles that of Ruta *et al.* (2013), which showed  
542 that amonodont therapsid disparity decreased steadily over time, relatively unaffected by  
543 the end-Permian mass extinction. More broadly, these findings might be said to agree  
544 with those of Lupia *et al.* (1999), which showed that the rate and character of change in  
545 the disparity of Late Cretaceous angiosperms was not altered by the end-Cretaceous mass  
546 extinction, and with Zelditch *et al.* (2003), whose work with piranha suggested that  
547 disparity tends naturally to decay over time. This scenario also shows that disparity and  
548 diversity were significantly decoupled in harpetids, which supports the idea that disparity  
549 and diversity are frequently decoupled (Foote 1993; Lupia 1999; Thorne *et al.* 2011;  
550 Hopkins 2013; Ruta *et al.* 2013).

551         The fact that harpetids in particular were relatively unaffected by the Late  
552 Ordovician mass extinction may perhaps be explained by their life history strategy.  
553 Harpetid larvae are thought to have been benthic rather than planktonic (Chatterton and  
554 Speyer 1989). In this they resemble sphaerexochine trilobites, which also had benthic  
555 larvae and were largely unaffected by the Late Ordovician mass extinction. Both of these  
556 examples agree with the general findings of Chatterton and Speyer (1989), who

557 concluded that trilobites with benthic larvae were generally far more resilient to the Late  
558 Ordovician mass extinction.

559         Despite their resilience, harpetid disparity remained low or continued to fall from  
560 the Late Ordovician onward, until the group went extinct at the end of the Devonian; no  
561 long-term recovery of disparity could be discerned (Fig. 4; Fig. 5). This finding is again  
562 consistent with Ruta *et al.* (2013) and also with Thorne *et al.* (2011), which found that  
563 ichthyosaurs failed to fully recover their former disparity following the end-Triassic mass  
564 extinction. These cases are analogous to that of a “Dead Clade Walking” or DCW  
565 (Jablonski 2002), where a clade that fails to recover in terms of taxonomic diversity  
566 following a mass extinction. However, the failure of a clade to recover in terms of  
567 disparity (rather than diversity) in the aftermath of an extinction event lacks a widely  
568 accepted name. The authors submit the term “Fixed Clade Walking” or FCW as a  
569 possible designation for such cases that would mirror the cadence of the term “Dead  
570 Clade Walking” while emphasizing a loss of morphological variability.

571         The concept of an FCW is related to, but not synonymous with, the concept of  
572 stabilomorphy (Kin and Błażejowski 2014). On its surface, an assessment of  
573 stabilomorphy simply observes that a group of organisms—like harpetids—remains  
574 relatively morphologically stable over time and space. However, Kin and Błażejowski  
575 (2014) also explicitly links stabilomorphy to successful adaptation, writing of  
576 stabilomorphs “...their level of adaptation, the quality of their adaptive strategy is so high  
577 (so effective), that small changes which had to continually occur over several millions  
578 years...did not result in any significant morphology variations.”

579 In contrast, the term “Fixed Clade Walking” claims no relationship between a loss  
580 of morphological variability and successful adaptation. Instead, an FCW implies a form  
581 of “survival without recovery” (Jablonski 2001). Following a major perturbation, an  
582 FCW is unable to generate new morphologies, not because their adaptive strategy is  
583 beyond improvement, but because changed conditions suppress further morphological  
584 innovation.

585 *Morphospace Through Time.* Studying harpetid morphospace provides additional insights  
586 (Fig. 6). Early in their history, harpetids’ morphospace occupation expands considerably  
587 (Fig. 6). PERMANOVA testing confirms that Cambrian and Ordovician harpetid  
588 morphospace were statistically significantly different (Table 2). These changes support  
589 an assessment of early diversification and moreover show that harpetids were very  
590 morphologically dynamic during their early history. However, this dynamicity seems to  
591 wane somewhat as the order enters the Silurian. Although Silurian and Ordovician  
592 harpetid morphospace remain statistically different, the significance of this difference has  
593 declined (Table 2). In particular, the area of morphospace occupied during the Late  
594 Ordovician is quite similar to that occupied throughout the Silurian. Yet the sum of  
595 variance does gradually decline (Fig. 4; Fig. 5), even while overall morphospace  
596 occupation changes little (Fig. 6). From this it seems clear that morphologies were being  
597 removed in a random, non-selective fashion (Korn *et al.* 2013). These losses were  
598 gradual, rather than occurring suddenly at the end of the Ordovician, indicating that  
599 harpetid morphospace was generally agnostic to the Late Ordovician mass extinction.

600 During the Devonian the centroid harpetid morphospace shifts once more, and the  
601 emergence of morphologically distinctive genera (*Eskoharpes* and *Globoharpes*) during

602 this time suggests that the order retained some ability to innovate. (Fig. 6). However, the  
603 scale of these shifts in morphospace is relatively small (Fig. 6) and overall measures of  
604 disparity continue their slow decline (Fig. 4; Fig. 5). Harpetids lose access to large areas  
605 of morphospace and never regain any of regions they held prior to the end of the  
606 Ordovician (Fig. 6). From this, it seems evident that harpetids became less  
607 morphologically dynamic over their history. Other researchers have observed that groups  
608 emerge from mass extinction events lacking the ability morphologically or ecologically  
609 diversify (Jablonski 2002; Thorne *et al.* 2011; Ruta *et al.* 2013). It is possible that,  
610 although the Late Ordovician mass extinction had little immediate impact on harpetid  
611 disparity, the biotic crisis nevertheless permanently damaged harpetids' ability to  
612 generate new morphologies, supporting our description of the order as a "Fixed Clade  
613 Walking". These findings emphasize that the impacts of a mass extinction event can be  
614 complex and may take many millions of years to fully unfold.

615 *Patterns of Morphospace Occupation.* The phylogenetic signal within harpetid  
616 morphospace appears strong. Statistically significant differences are found between the  
617 areas of morphospace occupied by all four putative harpetid families (Table 3). Of these,  
618 three families also group well along PCO 1 and PCO 2 (Fig. 7). The polyphyletic  
619 entomaspidids (perhaps unsurprisingly) do not group well (Fig. 7). This group also shows  
620 the least statistically significant difference with another harpetid family, in this case the  
621 harpidids (Table 3).

622 Harpetids associated with deep water habitats occupy significantly different areas  
623 of morphospace than those associated with shallow water habitats (Table 4). This finding  
624 is consistent with the work of Hopkins (2014), which revealed strong environmental

625 influence on patterns of disparity in trilobites, and emphasizes the way in which studies  
626 of disparity can bridge the gap between ecological and phylogenetic understandings of  
627 evolutionary history. One interesting detail of this analysis is that *Bowmania* emerges as a  
628 generalist harpetid, despite its unusual morphology. This places *Bowmania* into the same  
629 ecological category as taxa with a more generalized harpetid morphotype like *Harpes* and  
630 *Bohemoharpes*, which appear quite distantly from *Bowmaina* (Fig. 8). This may support  
631 the idea that *Bowmania* evolved a different solution to a recurring ecological problem,  
632 using a fringe of radiating spines in place of the familiar harpetid brim.

633

#### 634 **SYSTEMATIC PALAEOLOGY**

635 Class TRILOBITA Walch, 1771

636 Subclass LIBROSTOMA Fortey, 1990

637 Order HARPETIDA Whittington, 1959

638 *Diagnosis.* Cephalon subsemicircular to ovate in outline, with long genal prolongations  
639 (broad, flat) or spines (narrow, rounded). Glabella convex, narrowing forward, with up to  
640 three pairs of lateral glabellar furrows, preoccipital pair isolating triangular lateral lobes;  
641 occipital ring convex; preglabellar field sloping outward and downward to flat or  
642 upwardly concave fringe or bilamellar border; alae may be present; prominent eye lobes  
643 or tubercles centrally located on genae, with strong eye ridges and in some forms with  
644 genal ridges also; sutures commonly marginal except on dorsal side at genal angles, and  
645 (in genera with eye lobes) where sections of sutures run inward close together. Thorax  
646 with 12 or more segments; axis convex; pleurae flat, with broad pleural furrows.  
647 Pygidium short, subtriangular or elongate, with convex axis. Radiating, anastomosing

648 genal caecae may be present on genae and prelabellar field, and extending onto fringe;  
649 external surface of cephalon may be tuberculate or granulose (modified from Fortey and  
650 Owens 1997).

651 *Range.* Upper Cambrian to Upper Devonian.

652

653 Family 'ENTOMASPIDIDAE' Ulrich in Bridge, 1931

654 *Type genus.* *Entomaspis* Ulrich in Bridge, 1931.

655 *Included genera.* *Baikadamaspis* Ergaliev, 1980; *Entomaspis* Ulrich, 1931; *Notchpeakia*  
656 Adrain and Westrop, 2006.

657 *Diagnosis.* Exoskeleton small. Cephalon semicircular, characterized by anterior and  
658 posterior sections of facial sutures close to each other, both directed outward-backward;  
659 librigenae fused together through doublure, consisting of narrow dorsal strips connecting  
660 eyes to margin and genal spines (modified from Fortey and Owens 1997).

661 *Remarks.* The family Entomaspididae is resolved in the present analyses as polyphyletic  
662 and needs to be redefined so as to be monophyletic. The family is here used to denote  
663 various basal harpetids, with the quote marks denoting polyphyly.

664 *Range.* Upper Cambrian to Lower Ordovician.

665

666 Family HETERO-CARYONIDAE Hupé, 1953

667 *Type genus.* *Heterocaryon* Raymond, 1937.

668 *Included genera.* *Bowmania* Walcott, 1925; *Conococheaguea* Rasetti, 1959;

669 *Heterocaryon* Raymond, 1937.

670 *Diagnosis.* Angle of cephalic curvature greater than 90 degrees. Yoked librigenae, but  
671 lacking true bilamellar fringe. Facial sutures directed outward and forward. Small eye  
672 lobes, diverging posteriorly, with eye ridges anterolaterally directed. High cephalon  
673 convexity and equilateral glabellar lateral margins. Highly convex genae. Lacking alae.  
674 Narrow, rounded genal prolongations (i.e. spines). Pygidium of four to eight segments.  
675 *Remarks.* This family level name has been resurrected to describe a clade including the  
676 genus *Heterocaryon* and two other taxa previously assigned to Harpetidae but whose  
677 unusual morphology otherwise placed them within the entomaspidid grade in these  
678 phylogenetic analyses.  
679 *Range.* Upper Cambrian.

680

681 Family HARPIDIDAE Whittington, 1950

682 *Type genus.* *Harpides* Beyrich, 1846.

683 *Included genera.* *Chencunia* Qiu, 1984; *Dictyocephalites* Bergeron, 1895; *Harpides*  
684 Beyrich, 1846; *Kitatella* Petrunia in Khalfin, 1960; *Loganopeltis* Rasetti, 1943;  
685 *Loganopeltoides* Rasetti, 1945; *Metaharpides* Pillet and Courtessole, 1980; *Paraharpides*  
686 Pillet and Courtessole, 1980; *Pscemiaspis* Abdullaev, 1970.

687 *Diagnosis.* Cephalic border not sharply set off from convex genae and preglabellar field;  
688 alae small, semicircular; facial sutures marginal, or with parallel anterior and posterior  
689 sections running close to each other and directed anterolaterally from eye tubercles to  
690 margin; genal caeca radiating over cheek lobes and in some extending onto cephalic  
691 border. Hypostome subrectangular, length (*sag.*) equal to that of glabella. Thorax with 20  
692 or more segments; axis narrow; long (*tr.*) pleurae curving back at outer part may be

693 extended into spines, with deep pleural furrows and convex posterior bands (Fortey and  
694 Owens 1997).

695 *Range.* Upper Cambrian to Lower Ordovician.

696

697 Family HARPETIDAE Hawle and Corda, 1847

698 *Type genus.* *Harpes* Goldfuss, 1839.

699 *Included genera.* *Bohemoharpes* Vanek, 1963; *Brachyhipposiderus* Jell, 1985;  
700 *Dolichoharpes* Whittington, 1949; *Dubhglasina* Lamont, 1948; *Eoharpes* Raymond,  
701 1905; *Eskoharpes* McNamara et al., 2009; *Globoharpes* McNamara et al., 2009; *Harpes*  
702 Goldfuss, 1939; *Hibbertia* Jones and Woodward, 1898; *Kathrynia* Westrop, 1986;  
703 *Kielania* Vanek, 1963; *Lioharpes* Whittington, 1950; *Palaeoharpes* Lu and Qian in Zhou  
704 et al., 1977; *Scotoharpes* Lamont, 1948.

705 *Diagnosis.* Eye tubercles each with two lenses; semicircular alae adjacent to posterior  
706 glabellar lobes; bilamellar fringe with opposed pits in outer surfaces, genal rolls steeply  
707 sloping, brim gently sloping, with stout girder on lower lamella separating these two  
708 parts, flattened prolongations of fringe varying in length; cephalic suture skirts marginal  
709 band of fringe. Hypostome pear-shaped in outline, with ovate middle body, large anterior,  
710 small posterior, and wings. Thorax with 12 to 29 segments, pleurae bent down ventrally  
711 at tips. Pygidium small, short (*sag.*), triangular, with few segments. External surface of  
712 glabella and genae with raised ridges in reticulate pattern, tuberculate, or smooth; minute  
713 tubercles on fringe between pits and marginal band, on internal rim, and elsewhere  
714 (modified from Fortey and Owens 1997).

715 *Range.* Lower Ordovician to Upper Devonian.

716

717 **CONCLUSIONS**

718         The present study evaluates the morphology and evolution of harpetid trilobites, a  
719 group that had long been easily recognized but often incompletely understood. This study  
720 provides strong support for harpetid monophyly. Two of the three existing harpetid  
721 families have also been found to be monophyletic, while the third, Entomaspididae, has  
722 been found to be non-monophyletic. In addition, support has been found for the  
723 monophyly of a fourth harpetid family, the Heterocaryonidae, which unites several  
724 previously problematic taxa. At a finer taxonomic scale, several harpetid genera are  
725 found to be poorly supported (e.g. *Scotoharpes*, *Lioharpes*), while several others are  
726 found to be well supported (e.g. *Eskoharpes*, *Globoharpes*). Importantly, marginal  
727 sutures, a key innovation within Harpetida (Rasetti 1945; Ebach and McNamara 2002),  
728 are found to have arisen on at least two separate occasions within the order.

729         Harpetid disparity proves remarkably stable over geological time. A modest peak  
730 in the Ordovician is followed by a slow decline throughout the Silurian and Devonian.  
731 After the Ordovician, harpetids demonstrate little or no ability to colonize new areas of  
732 morphospace. This may represent a fundamental loss of morphological variability in the  
733 wake of the Late Ordovician mass extinction, a condition we here term “Fixed Clade  
734 Walking.” These findings demonstrate that mass extinction events may have complex  
735 impacts that play out over many millions of years, affecting not only species diversity but  
736 the range of living forms.

737

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747

#### 748 **SUPPORTING INFORMATION**

##### 749 *Appendix S1: Characters for Phylogenetic Analysis*

- 750 Character 1. Angle of cephalic curvature.  $>90$  degrees (0);  $\leq 90$  degrees (1).
- 751 Character 2. Cephalon convexity. Low (0); high (1).
- 752 Character 3. Widest point of cephalon. Posterior one-third (0); anterior one-third (1).
- 753 Character 4. Marginal rim demarcated along its inner margin by enlarged pits. Inner  
754 margin of rim not demarcated by enlarged pits (0); row of enlarged pits  
755 demarcates inner margin of rim (1).
- 756 Character 5. Bilamellar brim. Absent (0); present (1).
- 757 Character 6. Bilamellar brim profile. Flat (0); concave (1); convex (2).
- 758 Character 7. Brim width.  $<$  glabellar length (0);  $\geq$  glabellar length (1).

- 759 Character 8. Narrowing of brim along prolongations. Brim constant in width for the  
760 majority of prolongation (0); brim narrowing almost from the level of the  
761 occipital ring (1).
- 762 Character 9. Pitting present on outer field of cephalon/brim. Absent (0); present (1).
- 763 Character 10. Brim pitting extent. <50% of the brim surface visibly pitted (0); >50% of  
764 the brim surface visibly pitted (1).
- 765 Character 11. Radiating ridges at the genal roll-brim boundary. Absent (0); present (1).
- 766 Character 12. Girder separating genal rolls from brim. Absent (0); present (1).
- 767 Character 13. Girder kink. Absent (0); present (1).
- 768 Character 14. Deep pits along outer margin of genal roll. Absent (0); present (1).
- 769 Character 15. Position of hypostome constriction. Anterior one-fourth of hypostome (0);  
770 midpoint of hypostome (1).
- 771 Character 16. Median tubercle on frontal lobe. Absent (0); present (1).
- 772 Character 17. Preglabellar transverse ridge. Absent (0); present (1).
- 773 Character 18. Anterior prelabellar depression. Absent (0); present (1).
- 774 Character 19. Anterior boss. Absent (0); present (1).
- 775 Character 20. Anterior boss inflation. Slight inflation (0); bulbous, rising above the  
776 surrounding surface (1).
- 777 Character 21. Vaulted inner genal roll. Absent (0); present (1).
- 778 Character 22. Genal roll profile. Convex (0); concave (1).
- 779 Character 23. Glabellar morphology. Narrowing anteriorly (0); widening anteriorly (1).
- 780 Character 24. Depth of 1st pair of lateral glabellar furrows (S1). Deep, well defined (0);  
781 shallow, poorly defined (1).

- 782 Character 25. Morphology of S1. Posterolaterally directed furrows (0); J-shaped furrows  
783 not continuous with S0 (1).
- 784 Character 26. Second pair of lateral glabellar furrows (S2). Absent (0); present (1).
- 785 Character 27. Third pair of lateral glabellar furrows (S3). Absent (0); present (1).
- 786 Character 28. Length of 1st pair of lateral glabellar furrows (S1). <50% of glabellar  
787 width (0); >50% of glabellar width (1).
- 788 Character 29. Maximum length of S2 or S3. Long, c. 50% of glabella width (0); short, c.  
789 25% of glabella width (1).
- 790 Character 30. Positioning of S2 and S3. Well-spaced (0); S2 and S3 close together, third  
791 pair of glabellar lobes (L3) expanded (1).
- 792 Character 31. Cross-sectional morphology of glabellar furrows. Rounded (0); incised  
793 (1).
- 794 Character 32. Curvature of glabellar furrows S2–S3. Straight (0); incurving (curve  
795 posteriorly) (1); outcurving (curve anteriorly) (2).
- 796 Character 33. Glabellar lateral margins. Converging anteriorly (0); parallel (1).
- 797 Character 34. Relative volume of first pair of glabellar lobes (L1). L1 <10% of glabellar  
798 volume (0); L1 >10% of glabellar volume (1).
- 799 Character 35. Glabellar and genal primary surface ornament/sculpture. Tuberculate (0);  
800 reticulation of pits (1); fine granulations (2).
- 801 Character 36. Sagittal crest. Absent (0); present (1).
- 802 Character 37. Yoked librigenae. Absent (0); present (1).
- 803 Character 38. Facial suture position. Cuts through outer margin of cephalon (0); skirts  
804 margin (1).

- 805 Character 39. Angle of anterior facial suture and transverse line passing through both  
806 compound eyes. 30–45 degrees (0);  $\geq 60$  degrees (1);  $\leq 0$  degrees (2).
- 807 Character 40. Cephalic sutures with marked inward curve just posterior to cephalic  
808 margin. Absent (0); present (1).
- 809 Character 41. Eye structure. Eye lobes (0); tubercles (1).
- 810 Character 42. Angle formed by axis of greater elongation of eye with longitudinal axis  
811 of cephalon. Diverging posteriorly (0); equilateral (1).
- 812 Character 43. Lateral position of eye. Closer to alar furrow (0); closer to axial furrow  
813 (1).
- 814 Character 44. Anterior-posterior position of eye. On posterior of cephalon (0–45%) (0);  
815 on midline or anterior (48%+) (1); eye encompasses entire cephalon length  
816 (2).
- 817 Character 45. Genal ridge running postero-laterally from eye. Absent (0); present (1).
- 818 Character 46. Eye area in dorsal view (as percentage of cephalon). 20–30% (0);  $< 15\%$   
819 (1).
- 820 Character 47. Eye ridges. Absent (0); present (1).
- 821 Character 48. Eye ridge direction. Anterolaterally directed (0); posterolaterally directed  
822 (1); transversely directed (perpendicular to longitudinal axis of the body)  
823 (2).
- 824 Character 49. Ridge insertion on compound eye. Anterior point of eye (0); mid-point of  
825 eye (1).
- 826 Character 50. Genae curvature. Flattened/moderately convex (0); concave (1); extremely  
827 convex (2).

- 828 Character 51. Radiating, anastomosing genal caeca. Absent (0); present (1).
- 829 Character 52. Axial furrow depth. Shallow (0); deep (1).
- 830 Character 53. Extension of axial furrows beyond glabella onto genal roll. Absent (0);  
831 present (1).
- 832 Character 54. Alae. Absent (0); present (1).
- 833 Character 55. Alae strength as defined by alar furrow. Faint (shallow alar furrow) (0);  
834 strong (deep alar furrow) (1).
- 835 Character 56. Alae morphology. Subdivided into two crescentic portions by presence of  
836 interalar furrow (0); continuous, interalar furrow absent (1).
- 837 Character 57. Relief of alae. Depressed or sunken (0); flattened/low relief (1); inflated  
838 (2).
- 839 Character 58. Vaulting of inflated alae. Inflated alae not exhibiting vaulting (0); inflated  
840 alae vaulted (1).
- 841 Character 59. Alae size. Small ( $<L1$ ) (0); large ( $\geq L1$ ) (1).
- 842 Character 60. Alae direction. Transversely/laterally directed (0); anterolaterally directed  
843 (1).
- 844 Character 61. Large pits on genal area opposite alae. Absent or not enlarged (0); present  
845 and enlarged (1).
- 846 Character 62. Anterior alar ridge. Absent (0); present (1).
- 847 Character 63. Median tubercle on occipital ring. Absent (0); present (1).
- 848 Character 64. Genal spines or prolongations. Postero-lateral margin of cephalon  
849 extending into genal spines/prolongations (0); cephalon not extending into  
850 genal spines/prolongations (1).

- 851 Character 65. Cross-sectional morphology of genal spines or prolongations. Broad,  
852 flattened (prolongations) (0); narrow, rounded (spines) (1).
- 853 Character 66. Genal spine or prolongation curvature. Interior/proximal margin straight  
854 (0); interior/proximal margin incurving (1).
- 855 Character 67. Genal spine or prolongation angle of divergence. High ( $\geq 30$  degrees) (0);  
856 moderate (11 to 29 degrees) (1); reduced ( $\leq 10$  degrees) (2).
- 857 Character 68. Curvature of genal spines or prolongations. Straight (rapidly flattens from  
858 cephalon) (0); concave (twisted along length of prolongation) (1).
- 859 Character 69. Genal spine or prolongation length. Longer than cranidium (0); equal to or  
860 shorter than cranidium length (1).
- 861 Character 70. Thoracic axis width (at broadest point). < glabellar width (0); = glabellar  
862 width (1); > glabellar width (2).
- 863 Character 71. Free thoracic tergite count.  $\leq 15$  (0);  $\geq 16$  (1).
- 864 Character 72. Form of pleural spine terminations on thoracic tergites. Acute, spinous (0);  
865 blunt (1).
- 866 Character 73. Pygidium with medial posterior indentation. Absent (0); present (1).
- 867 Character 74. Number of axial rings in pygidium. 4–5 (0); 3 (1); 2 (2); 7–8 (3).
- 868 Character 75. Pleural field margin. Downturned (0); upturned (1); flat (2).
- 869 Character 76. Terminal lappets. Absent (0); present (1).

870

#### 871 **DATA ARCHIVING STATEMENT**

872 Data for this study, including a full set of character state illustrations are available in

873 MorphoBank: <http://morphobank.org/permalink/?P2804> [login with user name 2804;

874 password “papersINpalaeontology”] [please note that the data for this paper are not yet  
875 published and this temporary link should not be shared without the express permission of  
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877

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884

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886 JCL conceived of the initial study; JDB and JCL developed the study; JDB gathered the  
887 study data; JDB performed analyses with input from JCL; JDB and JCL interpreted the  
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## 889 **REFERENCES**

- 890 ABDULLAEV, R. N. and KHALETSKAYA, O. N. 1970. Lower Paleozoic of the  
891 Chatkalskiy Range: Trilobites and graptolites of the Ordovician of the Pskemskiy  
892 Range. Institut Geologii i Geofiziki, Uzbek SSR, Tashkent. 104 pp.
- 893 ADRAIN, J. M. 2011. Class Trilobita. *Animal Biodiversity: Zootaxa*. **3148**, 104–109.
- 894 ---, EDGECOMBE, G. D., FORTEY, R. A., HAMMER, O., LAURIE, J. R.,  
895 MCCORMICK, T., OWEN, A. W., WAISFELD, B. G., WEBBY, B. D.,  
896 WESTROP, S. R. and ZHOU., Z. 2004. Trilobites. 231–254. *In* WEBBY, B. D.,

897 PARIS, F., DROSER, M. L. and PERCIVAL, I. G. (eds.). *The great Ordovician*  
898 *biodiversification event*. Columbia University Press, New York, NY, 496 pp.

899 --- and WESTROP, S. R. 2004. A Late Cambrian (Sunwaptan) silicified trilobite fauna  
900 from Nevada. *Bulletins of American Paleontology*. **365**, 5–56.

901 --- and WESTROP, S. R. 2006. Notchpeakia, a new genus of Upper Cambrian  
902 (Sunwaptan) “entomaspidid” trilobites. *Journal of Paleontology*. **80**, 1152–1171.

903 ANDERSON, M. J. 2017. Permutational Multivariate Analysis of Variance  
904 (PERMANOVA). In BALAKRISHNAN, N., COLTON, T., EVERITT, B.,  
905 PIEGORSCH, W., RUGGERI, F. and TEUGELS, J. (eds.). *Wiley StatsRef:*  
906 *Statistics Reference Online*. Online: John Wiley and Sons, Ltd.

907 ARMSTRONG, R. A. 2014. When to use the Bonferroni correction. *OPO*. **34**, 502–508.

908 BAMBACH, R. K., KNOLL, A. H. and WAMG, S. C. 2004. Origination, extinction, and  
909 mass depletions of marine diversity. *Paleobiology*. **30**, 522–542.

910 BAPST, D. W., BULLOCK, P. C., MELCHIN, M. J., SHEETS, H. D. and MITCHELL,  
911 C. E. 2012. Graptoloid diversity and disparity became decoupled during the  
912 Ordovician mass extinction. *Proceedings of the National Academy of Sciences*.  
913 **109**, 3428–33.

914 BERGERON, J. N. 1895. Notes paléontologiques. *Bulletin de la Société Géologique de*  
915 *France, 3rd series*. 23, 4–5.

916 BEYRICH, E. 1846. Untersuchungen über Trilobiten. Zweite Stück als Fortsetzung zu  
917 der Abhandlung “Ueber einiger böhmische Trilobiten”. Berlin. 37 pp.

918 BRENCHLEY, P. J., CARDEN, G. A., HINTS, L., KALJO, D., MARSHALL, J. D.,  
919 MARTMA, T., MEIDLA, T. and NÖLVAK, J. 2003. High resolution stable

920 isotope stratigraphy of Upper Ordovician sequences: constraints on the timing of  
921 bioevents and environmental changes associated with mass extinction and  
922 glaciation. *Geological Society of American Bulletin*. **115**, 89–104.

923 BRIDGE, J. 1931. Geology of the Eminence and Cardareva Quadrangles. *Missouri*  
924 *Bureau of Geology and Mines, 2nd series*. **24**, 1–228.

925 BRIGGS, D. E. G., FORTEY, R. A., and WILLS, M. A. 1992. Morphological Disparity  
926 in the Cambrian. *Science*. **256**, 1670–1673.

927 BRUSATTE, S. L., MONTANARI, S., YI, H. and NORELL, M. A. 2011. Phylogenetic  
928 corrections for morphological disparity analysis: new methodology and case  
929 studies. *Paleobiology*. **37**, 1–22.

930 CHATTERTON, B. D. E. and SPEYER, S. E. 1989. Larval ecology, life history  
931 strategies, and patterns of extinction and survivorship among Ordovician  
932 trilobites. *Paleobiology*. **15**, 118–132.

933 CONGREVE, C. R. 2008. The End Ordovician; an ice age in the middle of a greenhouse.  
934 9–19. In ELEWA, A. M. T. (ed.). *Mass Extinction*. Springer, Berlin, Heidelberg,  
935 252 pp.

936 --- 2013a. Cladal Turnover: the end-Ordovician as a large-scale analogue of species  
937 turnover. *Palaeontology*. **56**, 1285–1296.

938 --- 2013b. Evolutionary patterns of trilobites across the end Ordovician mass extinction.  
939 (Thesis). University of Kansas.

940 ---, FALK, A. R. and LAMSDELL, J. C. 2018. Biological hierarchies and the nature of  
941 extinction. *Biological Reviews*. **93**, 811–826.

942 ---, KRUG, A. Z. and PATZKOWSKY, M. E. 2019. Evolutionary and biogeographical  
943 shifts in response to the Late Ordovician mass extinction. *Palaeontology*. **62**,  
944 267–285.

945 --- and LAMSDELL, J. C. 2016. Implied weighting and its utility in palaeontological  
946 datasets: a study using modelled phylogenetic matrices. *Palaeontology*. **59**, 447–  
947 462.

948 --- and LIEBERMAN, B. S. 2011. Phylogenetic and biogeographic analysis of  
949 sphaerexochine trilobites. *Public Library of Science One*. **6**, e21304.

950 CRÔNIER, C. 2007. Larval morphology and ontogeny of an Upper Devonian phacopid:  
951 Nephranops from Thuringia, Germany. *Journal of Paleontology*. **81**, 684–700.

952 --- 2010. Varied development of trunk segmentation in three related Upper Devonian  
953 phacopine trilobites. *Historical Biology*. **22**, 341–347.

954 --- 2013. Morphological disparity and development patterning: contribution of phacopid  
955 trilobites. *Palaeontology*. **56**, 1263–1271.

956 ---, AUFFRAY, J. C. and COURVILLE, P. 2005. A quantitative comparison of the  
957 ontogeny of two closely-related Upper Devonian phacopid trilobites. *Lethaia*, **38**,  
958 123–135.

959 ---, BIGNON, A. and FRANCOIS, A. 2011. Morphological and ontogenetic criteria for  
960 defining a trilobite species: the example of Siluro-Devonian Phacopidae. *Comptes*  
961 *Rendus Palevol*. **10**, 143–153.

962 --- and COURVILLE, P. 2003. Variations du rythme du developpement chez les  
963 trilobites Phacopidae neodevoniens. *Comptes Rendus Palevol*. **2**, 577–585.

964 --- and FORTEY, R. A. 2006. Morphology and ontogeny of an Early Devonian phacopid  
965 trilobite with reduced sight from southern Thailand. *Journal of Paleontology*. **80**,  
966 529–536.

967 DAI, T. AND ZHANG, X. 2013. Ontogeny of the redlichiid trilobite *Eoredlichia*  
968 *intermedia* from the Chengjiang Lagerstätte, lower Cambrian, southwest China.  
969 *Lethaia*. **46**, 262–273.

970 DELINE, B., GREENWOOD, J.M., CLARK, J.W., PUTTICK, M.N., PETERSON, K.J.,  
971 and DONOGHUE, P.C.J. 2018. Evolution of metazoan morphological disparity.  
972 *Proceedings of the National Academy of Sciences*. **115**, 8909–8918.

973 DIRZO, R., YOUNG, H. S., GALETTI, M., CEBALLOS, G., ISAAC, N. J. B. and  
974 COLLEN, B. 2014. Defaunation in the Anthropocene. *Science*. **345**, 401–406.

975 DOMMERGUES, J., LUAIRN, B. and MEISTER, C. 1996. Evolution of ammonoid  
976 morphospace during the Early Jurassic radiation. *Paleobiology*. **22**, 219–240.

977 DROSSER, M. L., BOTTJER, D. J., SHEEHAN, P. M. and MCGHEE, G. R. 2000.  
978 Decoupling of taxonomic and ecologic severity of Phanerozoic marine mass  
979 extinctions. *Geology*. **28**, 675–678.

980 DUNN, O. J. 1961. Multiple Comparisons among Means. *Journal of the American*  
981 *Statistical Association*. **293**, 52–64.

982 EBACH, M. C. and MCNAMARA, K. J. 2002. A systematic revision of the family  
983 Harpetidae (Trilobita). *Records of the Western Australian Museum*. **21**, 135–167.

984 ERGALIEV, G. K. 1980. Trilobity srednego i verkhnego Kembriya Malogo Karatau  
985 (Middle and Upper Cambrian trilobites from Malyy Karatau). *Akademiya Nauk*  
986 *Kazakhskoi, SSR, Alma-Ata*. 211 pp.

- 987 FATKA, O., MERGAL, M. and BUDIL, P. 2013. Preservation of the digestive structures  
988 in Harpides (Trilobita) from the Lower Ordovician of the Barrandian area (Czech  
989 Republic). *Neues Jahrbuch für Geologie und Paläontologie*. **270**, 1–15.
- 990 FINNEGAN, S., BERGMANN, K., EILER, J. M., JONES, D. S., FIKE, D. A.,  
991 EISENMAN, I., HUGHES, N. C., TRIPATI, A. K. and FISCHER, W. W. 2011.  
992 The magnitude and duration of Late Ordovician-Early Silurian glaciation.  
993 *Science*. **331**, 903–906.
- 994 ---, HEIM, N. A., PETERS, S. E. and FISCHER, W. W. 2012. Climate change and the  
995 selective signature of the Late Ordovician mass extinction. *Proceedings of the  
996 National Academy of Sciences*. **109**, 6829–6834.
- 997 ---, RASMUSSEN, C. M. Ø, and HARPER, D. A. T. 2016. Biogeographic and  
998 bathymetric determinants of brachiopod extinction and survival during the Late  
999 Ordovician mass extinction. *Proceedings of the Royal Society B*. **283**, 1–9.
- 1000 FITCH, W. M. 1997. Toward Defining the Course of Evolution: Minimum Change for a  
1001 Specific Tree Topology. *Systematic Zoology*. **20**, 406–416.
- 1002 FOOTE, M. 1991a. Analysis of Morphological Data. *The Paleontological Society  
1003 Papers*. **4**, 59–86.
- 1004 --- 1991b. Morphological and taxonomic diversity in a clade's history: the blastoid record  
1005 and stochastic simulations. *Contributions from the Museum of Paleontology*. **28**,  
1006 101–140.
- 1007 FOOTE, M. 1992a. Rarefaction analysis of morphological and taxonomic diversity.  
1008 *Paleobiology*. **18**, 17–29.

1009 --- 1992b. Paleozoic record of morphological diversity in blastozoan echinoderms.  
1010 *Proceedings of the National Academy of Sciences*. **89**, 7325–7329.

1011 --- 1993. Discordance and concordance between morphological and taxonomic diversity.  
1012 *Paleobiology*. **19**, 185–204.

1013 --- 1994. Morphological disparity in Ordovician-Devonian crinoids and the early  
1014 saturation of morphological space. *Paleobiology*. **20**, 320–344.

1015 --- 1995. Morphological Diversification of Paleozoic Crinoids. *Paleobiology*. **21**, 273–  
1016 299.

1017 --- The evolution of morphological diversity. *Annual Review of Ecological Systematics*.  
1018 **28**, 129–152.

1019 --- Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic  
1020 crinoids. *Paleobiology*. **25**, 1–115.

1021 FORTEY, R. A. 1990. Ontogeny, hypostome attachment and trilobite classification.  
1022 *Palaeontology*. **33**, 529–576.

1023 --- and OWENS, R. M. 1997. Evolutionary history. 250–287. In KAESLER, R. L. (ed.).  
1024 *Treatise on Invertebrate Paleontology, part O, Arthropoda 1, Trilobita, (revised)*.  
1025 Geological Society of America, Boulder, CO & University of Kansas Press,  
1026 Lawrence, KS, 530 pp.

1027 --- and OWENS, R. M. 1999. Feeding habits in trilobites. *Palaeontology*. 42(3): 429–  
1028 465.

1029 GARAMSZEGI, L. 2006. Comparing effect sizes across variables: generalization without  
1030 the need for Bonferroni correction. *Behavioral Ecology*. **17**, 682–687.

- 1031 GOLDFUSS, A. 1839. Beiträge zur Petrefactenkunde. *Verhandlungen der Kaiserlichen*  
1032 *Leopoldinisch-Carolinischen der Naturforscher*. **19**, 327–364.
- 1033 GOLOBOFF, P. A., FARRIS, J. S. and NIXON, K. C. 2008. TNT, a free program for  
1034 phylogenetic analysis. *Cladistics*. **24**, 774–786.
- 1035 GOULD, S. J. 1991. The disparity of the Burgess Shale arthropod fauna and the limits of  
1036 cladistics analysis: why we must strive to quantify morphospace. *Paleobiology*.  
1037 **17**, 411–423.
- 1038 GOWER, J. C. 1971. A general coefficient of similarity and some of its properties.  
1039 *Biometrics*. **27**, 857–871.
- 1040 GUILLERME, T., COOPER, N., BRUSATTE, S. L., DAVIS, K. E., JACKSON, A. L.,  
1041 GERBER, S., GOSWAMI, A., HEALY, K., HOPKINS, M. J., JONES, M. E. H.,  
1042 LLOYD, G. T., O'REILLY, J. E., PATE, A., PUTTICK, M. N., RAYFIELD, E.  
1043 J., SAUPE, E. E., SHERRATT, E., SLATER, G. J., WEISBECKER, V.,  
1044 THOMAS, G. H., and DONOGHUE, P. C. J. 2020. Disparities in the analysis of  
1045 morphological disparity. *Biology Letters*. **16**, 1–8.
- 1046 HALLIDAY, T. J. D. and GOSWAMI, A. 2015. Eutherian morphological disparity  
1047 across the end-Cretaceous mass extinction. *Biological Journal of the Linnean*  
1048 *Society*. 118: 152–168.
- 1049 HAMMER, Ø. HARPER, D. A. T., and RYAN, P. D. 2001. PAST: paleontological  
1050 statistics software package for education and data analysis. *Palaeontologia*  
1051 *Electronica*. **4**, 9 pp.

1052 HARPER, D. A. T., HAMMARLUND, E. U. and RASMUSSEN, C. M. Ø. 2014. End  
1053 Ordovician extinctions: A coincidence of causes. *Gondwana Research*. **25**, 1294–  
1054 1307.

1055 HAWLE, I. and CORDA, A. J. C. 1847. Prodrum einer Monographie der böhmischen  
1056 Trilobiten. *Abhandlungen Kongl. Böhmerischen Gesellschaft der*  
1057 *Wissenschaften, V. Folge*. **5**, 1–176.

1058 HETHERINGTON, A. J., SHERRATT, E., RUTA, M., WILKINSON, M., DELINE, B.  
1059 and DONOGHUE, P. C. J. 2015. Do cladistic and morphometric data capture  
1060 common patterns of morphological disparity? *Palaeontology*. **58**, 393–399.

1061 HOPKINS, M. J. 2013. Decoupling of taxonomic diversity and morphological disparity  
1062 during decline of the Cambrian trilobite family Pterocephaliidae. *Journal of*  
1063 *Evolutionary Biology*. **26**, 1665–1676.

1064 --- 2014. The environmental structure of trilobite morphological disparity. *Paleobiology*.  
1065 **40**, 352–373.

1066 --- and GERBER, S. 2017. Morphological Disparity. 1–12. In NUNO DE LA ROSA L.,  
1067 MÜLLER, G. (eds.). *Evolutionary Developmental Biology*. Springer, Cham.

1068 --- and LIDGARD, S. 2012. Evolutionary mode routinely varies among morphological  
1069 traits within fossil species lineages. *Proceedings of the National Academy of*  
1070 *Sciences*. **109**, 20520–20525.

1071 HOU, X., CLARKSON, E. N. K., YANG, J., ZHANG, X., WU, G. and YUAN, Z. 2008.  
1072 Appendages of early Cambrian Eoredlichia (Trilobita) from the Chengjiang biota,  
1073 Yunnan, China. *Earth and Environmental Science Transactions of the Royal*  
1074 *Society of Edinburgh*. **99**, 213–223.

- 1075 HUELSENBECK, J. P. and RONQUIST, F. 2001. MRBAYES: Bayesian inference of  
1076 phylogenetic trees. *Bioinformatics*. **17**, 754–755.
- 1077 HUGHES, M., GERBER, S. and WILLS, M. A. 2013. Clades reach highest  
1078 morphological disparity early in their evolution. *Proceedings of the National*  
1079 *Academy of Sciences*. **110**, 13875–13879.
- 1080 HUGHES, N. C. 2007. The evolution of trilobite body patterning. *Annual Review of*  
1081 *Earth and Planetary Sciences*. **35**, 401–434.
- 1082 HUPÉ, P. 1953. Classification des trilobites. *Annales paleontologie*. **39**, 59–168.
- 1083 JABLONSKI, D. and RAUP, D. M. 1995. Selectivity of end-Cretaceous marine bivalve  
1084 extinctions. *Science*. **268**, 389–391.
- 1085 --- 2001. Lessons from the past: Evolutionary impacts of mass extinctions. *Proceedings*  
1086 *of the National Academy of Sciences*. **98**, 5393–5398.
- 1087 --- 2002. Survival without recovery after mass extinctions. *Proceedings of the National*  
1088 *Academy of Sciences*. **99**, 8139–8144.
- 1089 JELL, P. A. 1985. Tremadoc trilobites of the Digger Island Formation, Waratah Bay,  
1090 Victoria. *Memoirs of the Museum of Victoria*. **46**, 53–88.
- 1091 JELL, P. A. and ADRAIN, J. M. 2002. Available generic names for trilobites. *Memoirs*  
1092 *of the Queensland Museum*. **48**, 331–553.
- 1093 JONES, T. R. and WOODWARD, H. 1898. A monograph of the Palaeozoic Phyllopoda  
1094 (Phyllocarida, Packard). *Monographs of the Palaeontographical Society*. **3**, 125–  
1095 176.

- 1096 KHALFIN, L. L. 1960. (ed.). Palaeozoic biostratigraphy of the Sayan-Altay mountain  
1097 range. Vol 1: Lower Palaeozoic. Trudy Sibirskogo Nauchno-Issledovatel'skogo.  
1098 Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya. **19**, 1–498.
- 1099 KIESSLING, W. and ABERHAN, M. 2007. Environmental determinants of marine  
1100 benthic biodiversity dynamics through Triassic–Jurassic time. *Paleobiology*. **33**,  
1101 414–434.
- 1102 KIN, A. and BŁAŻEJOWSKI, B. 2014. The Horseshoe Crab of the Genus *Limulus*:  
1103 Living Fossil or Stabilomorph? *Public Library of Science One*. **9**, e108036.
- 1104 KORN, D., HOPKINS, M. J. and WALTON, S. A. 2013. Extinction space: a method for  
1105 the quantification and classification of changes in morphospace across extinction  
1106 boundaries. *Evolution*. **67**, 2795–2810.
- 1107 LAMONT, A. 1948. Scottish dragons. *The Quarry Manager's Journal*. **31**, 531–535.
- 1108 LAMSDELL, J. C. and SELDEN, P. A. 2014. Phylogenetic support for the monophyly of  
1109 proetide trilobites. *Lethaia*. **48**, 1–12.
- 1110 --- and SELDEN, P. A. 2017. From success to persistence: Identifying an evolutionary  
1111 regime shift in the diverse Paleozoic aquatic arthropod group Eurypterida, driven  
1112 by the Devonian biotic crisis. *Evolution*. **71**, 95–110.
- 1113 LEWIS, P. O. 2001. A likelihood approach to estimating phylogeny from discrete  
1114 morphological character data. *Systematic Biology*. **50**, 913–925.
- 1115 LLOYD, G. T. 2016. Estimating morphological diversity and tempo with discrete  
1116 character-taxon matrices: implementation, challenges, progress, and future  
1117 directions. *Biological Journal of the Linnean Society*. **118**, 131–151.

1118 LOFGREN, A. S., PLOTNICK, R. E. and WAGNER, P. J. 2003. Morphological  
1119 diversity of Carboniferous arthropods and insights on disparity patterns through  
1120 the Phanerozoic. *Paleobiology*. **29**, 349–368.

1121 LU, Y. 1940. On the ontogeny and phylogeny of *Redlichia intermediata* Lu (sp. nov.).  
1122 *Bulletin of the Geological Society of China*. **20**, 333–341.

1123 LUPIA, R. 1999. Discordant morphological disparity and taxonomic diversity during the  
1124 Cretaceous angiosperm radiation: North American pollen record. *Paleobiology*.  
1125 **25**, 1–28.

1126 MADDISON, W. P. and MADDISON, D. R. 2018. Mesquite: a modular system for  
1127 evolutionary analysis. Version 3.51 <http://www.mesquiteproject.org>

1128 MCCLAIN, C. R. 2005. Bathymetric patterns of morphological disparity in deep sea  
1129 gastropods from the western North Atlantic Basin. *Evolution*. **59**, 1492–1499.

1130 MCGHEE, G. R., SHEEHAN, P. M., BOTTJER, D. J. and DROSER, M. L. 2004.  
1131 Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic  
1132 severities are decoupled. *Palaeogeography, Palaeoclimatology, Palaeoecology*.  
1133 **211**, 289–297.

1134 ---, SHEEHAN, P. M., BOTTJER, D. J. and DROSER, M. L. 2012. Ecological ranking  
1135 of Phanerozoic biodiversity crises: The Serpukhovian (early Carboniferous) crisis  
1136 had a greater ecological impact than the end-Ordovician. *Geology*. **40**, 147–150.

1137 MCNAMARA, K. J., FEIST, R. and EBACH, M. C. 2009. Patterns of evolution and  
1138 extinction in the last harpetid trilobites during the late Devonian (Frasnian).  
1139 *Palaeontology*. **52**, 11–33.

- 1140 MORAN, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological  
1141 studies. *Oikos*. **100**, 403–405.
- 1142 NAKAGAWA, S. 2004. A farewell to Bonferroni: the problems of low statistical power  
1143 and publication bias. *Behavioral Ecology*. **15**, 1044–1045.
- 1144 NORFORD, B. S. 1973. Lower Silurian species of the trilobite *Scotoharpes* from Canada  
1145 and northwestern Greenland. *Contributions to Canadian Paleontology*. **1**, 9–25.
- 1146 PALMER, A. R. 1954. The faunas of the Riley Formation in central Texas. *Journal of*  
1147 *Paleontology*. **28**, 709–786.
- 1148 PEARSON, K. 2017. Experimental biomechanics of trinucleid fringe pits (Trilobita).  
1149 (Thesis). Oberlin College, OH, United States.
- 1150 PILLET, J. and COURTESSOLE, R. 1981. Revision de Harpides (Dictyocephalites)  
1151 villebruni (Bergéron 1895) (trilobite, Arenigien inferieur de la Montagne Noire,  
1152 France meridionale). *Bulletin de la Société Géologique de France*. **22**, 413–420.
- 1153 QIU, H. 1984. Trilobites from the Upper Cambrian Tangcun Formation in Jingxian,  
1154 southern Anhui. *Acta Palaeontologica Sinica*. **23**, 329–341.
- 1155 RASETTI, F., 1943. New Lower Ordovician trilobites from Levis, Quebec. *Journal of*  
1156 *Paleontology*. **17**, 101–104.
- 1157 RASETTI, F. 1945. Evolution of the facial sutures in the trilobites *Loganopeltoides* and  
1158 *Loganopeltis*. *American Journal of Science*. **243**, 44–50.
- 1159 --- 1952. Cephallic sutures in the Upper Cambrian trilobite *Entomaspis*. *Journal of*  
1160 *Paleontology*. **26**, 797–802.
- 1161 --- 1959. Trempealeauian trilobites from the Conococheague, Frederick, and Grove  
1162 Limestones of the Central Appalachians. *Journal of Paleontology*. **33**, 375–398.

- 1163 RASMUSSEN, C. M. Ø., KRÖGER, B., NIELSEN, M. L. and COLMENAR, J. 2019.  
1164 Cascading trend of Early Paleozoic marine radiations paused by Late Ordovician  
1165 extinctions. *Proceedings of the National Academy of Sciences*. **116**, 1–7.
- 1166 RAUP, D. M. 1992. *Extinction: bad genes or bad luck?* W.W. Norton, New York, NY,  
1167 210 pp.
- 1168 --- and SEPKOSKI, J. J. 1982. Mass extinctions in the marine fossil record. *Science*. **215**,  
1169 1501–1503.
- 1170 RAW, F. 1949. Facial sutures in the (hypoparian) trilobites *Loganopeltoides* and  
1171 *Loganopeltis*, and the validity of these genera. *Journal of Paleontology*. **23**, 510–  
1172 514.
- 1173 RAYMOND, P.E. 1905. Note on the names *Amphion*, *Harpina* and *Platymetopus*.  
1174 *American Journal of Science*. **19**, 377–378.
- 1175 RAYMOND, P.E. 1937. Upper Cambrian and Lower Ordovician Trilobita and Ostracoda  
1176 from Vermont. *Bulletin of the Geological Society of America*. **48**, 1079–1146.
- 1177 ROBISON, R. A. and BABCOCK, L. E. 2011. Systematics, paleobiology, and  
1178 taphonomy of some exceptionally preserved trilobites from Cambrian lagerstätten  
1179 of Utah. *Paleontological Contributions*. **5**, 1–47.
- 1180 ROY, K. and FOOTE, M. 1997. Morphological approaches to measuring biodiversity.  
1181 *Trends in Ecology and Evolution*. **12**, 277–281.
- 1182 RUTA, M., ANGIELCZYK, K. D., FRÖBISCH, J. and BENTON, M. J. 2013.  
1183 Decoupling of morphological disparity and taxic diversity during the adaptive  
1184 radiation of anomodont therapsids. *Proceedings of the Royal Society B*. **280**, 1–9.

- 1185 SCLAFANI, J. A., CONGREVE, C. R., KRUG, A. Z. and PATZKOWSKY, M. E. 2019.  
1186 Effects of mass extinction and recovery dynamics on long-term evolutionary  
1187 trends: a morphological study of Strophomenida (Brachiopoda) across the Late  
1188 Ordovician mass extinction. *Paleobiology*. **44**, 603–619.
- 1189 SEPKOSKI, J. J. 1996. Patterns of Phanerozoic extinction: a perspective from global data  
1190 bases. 35–51. In WALLISER, O. H., (ed.). *Global Events and Event Stratigraphy*  
1191 *in the Phanerozoic*. Springer, Berlin, Heidelberg, 333 pp.
- 1192 SHEEHAN, P. M. 1973. The relation of Late Ordovician glaciation to the Ordovician-  
1193 Silurian changeover in North American brachiopod faunas. *Lethaia*. **6**, 147–154.
- 1194 --- 2001. The late Ordovician mass extinction. *Annual Review of Earth and Planetary*  
1195 *Sciences*. **29**, 331–364.
- 1196 SIMON, M. S., KORN, D., and KOENEMEN, S. 2010. Disparity fluctuations in Jurassic  
1197 ammonoids by means of conch geometry. *Palaeogeography, Palaeoclimatology,*  
1198 *Palaeoecology*. **292**, 520–531.
- 1199 SOKAL, R. R., and ROHLF, F. J. 1995. Biometry. 3rd ed. W. H. Freeman and Company,  
1200 New York, 88 pp.
- 1201 SWOFFORD, D. L. and OLSEN, G. J. 1990. Phylogeny reconstruction. 411–501. In  
1202 HILLIS, D. M. and MORITZ, C. (eds.). *Molecular systematics*. Sinauer  
1203 Associates, Sunderland, MA, 588 pp.
- 1204 SUNDBERG, F.A. 1996. Morphological diversification of Ptychopariida (Trilobita) from  
1205 the Marjumiid biomere (Middle and Upper Cambrian). *Paleobiology*. **22**, 49–65.

- 1206 THORNE, P. M., RUTA, M. and BENTON, M. J. 2011. Resetting the evolution of  
1207 marine reptiles at the Triassic-Jurassic boundary. *Proceedings of the National*  
1208 *Academy of Sciences*. **108**, 8339–8344.
- 1209 VALENTINE, J. W. 1995. Why no new phyla after the Cambrian? Genome and ecospace  
1210 hypotheses revisited. *Palaios*. **10**, 190–194.
- 1211 VANEK, J. 1963. Nové rody z celedi Harpidae Hawle et Corda, 1847 (Trilobitae) z  
1212 Barrandienu. *Casopis Národního Muzea, Oddíl Přírodovedny*. **132**, 226–229.
- 1213 VILLIER, L. and EBLE, G. J. 2004. Assessing the robustness of disparity estimates: the  
1214 impact of morphometric scheme, temporal scale, and taxonomic level in  
1215 spatangoid echinoids. *Paleobiology*. **30**, 652–665.
- 1216 WAGNER, P. J. 1995. Testing evolutionary constraint hypotheses with early Paleozoic  
1217 gastropods. *Paleobiology*. **21**, 248–272.
- 1218 WALCH, J. E. I. 1771. Die naturgeschichte der verteinerungen, Dritter Theil. *Zur*  
1219 *erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur*. P.J.  
1220 Felstecker, Nürnberg. 235 pp.
- 1221 WALCOTT, C. D. 1925. Cambrian and Lower Ozarkian trilobites. *Smithsonian*  
1222 *Miscellaneous Collections*. **75**, 61–146.
- 1223 WESLEY-HUNT, G. D. 2005. The morphological diversification of carnivores in North  
1224 America. *Paleobiology*. **31**, 35–55.
- 1225 WESTROP, S.R. 1986. Late Cambrian and earliest Ordovician trilobites, southern  
1226 Canadian Rocky Mountains, Alberta. (Dissertation). University of Toronto,  
1227 Toronto, Canada.

- 1228 WESTROP, S. R. 1992. Upper Cambrian (Marjuman-Steptoean) trilobites from the Port  
1229 au Port Group, Western Newfoundland. *Journal of Paleontology*. **66**, 228–255.
- 1230 WHITTINGTON, H. B. 1949. *Dolichoharpes* and the origin of the harped fringe.  
1231 *American Journal of Science*. **247**, 276–285.
- 1232 WHITTINGTON, H. B. 1950. A monograph of the British trilobites of the family  
1233 Harpidae. *Monographs of the Palaeontographical Society*. **447**, 1–55.
- 1234 --- 1959: Silicified Middle Ordovician trilobites: Remopleuridae, Trinucleidae,  
1235 Raphiophoridae, Endymioniidae. *Bulletin of the Museum of Comparative*  
1236 *Zoology*. **121**, 371–496.
- 1237 WILLS, M. A. 1998. Crustacean disparity through the Phanerozoic: comparing  
1238 morphological and stratigraphic data. *Biological Journal of the Linnean Society*.  
1239 **65**, 455–500.
- 1240 ---, BRIGGS, D. E. G. and FORTEY, R. A. 1994. Disparity as an evolutionary index: a  
1241 comparison of Cambrian and Recent arthropods. *Paleobiology*. **20**, 93–130.
- 1242 WRIGHT, A. M. and HILLIS, D. M. 2014. Bayesian analysis using a simple likelihood  
1243 model outperforms parsimony for estimation of phylogeny from discrete  
1244 morphological data. *Public Library of Science One*. **9**, 1–6.
- 1245 YOUNG, M. T., BRUSATTE, S. L., RUTA, M. and DE ANDRADE, M. B. 2010. The  
1246 evolution of Metriorhynchoidea (Mesoeucrocodylia, Thalattosuchia): an  
1247 integrated approach using geometric morphometrics, analysis of disparity, and  
1248 biomechanics. *Zoological Journal of the Linnean Society*. **158**, 801–859.
- 1249 ZELDITCH, M. L., SHEETS, H. D. and FINK, W. L. 2003. The ontogenetic dynamics of  
1250 shape disparity. *Paleobiology*. **29**, 139–156.

1251 ZHOU, T., LIU, Y., MONG, X. and SUN, Z. 1977. Trilobites. 104–266. In WANG, X.  
1252 (ed.) *Atlas of the Palaeontology of South Central China, Volume 1, Early*  
1253 *Palaeozoic*. Geological Publishing House, Beijing, 470 pp.

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## 1255 **EXPLANATIONS OF FIGURES AND TABLES**

1256 FIG. 1. Fossil trilobites of the order Harpetida. A: *Lioharpes venulosus*, B:  
1257 *Dolichoharpes dentoni* (?), C: *Kielania dorbignyana*, D: *Bohemoharpes ungula*, E:  
1258 *Scotoharpes spasskii*, F: *Hibbertia wegelini*. 1 cm scale bar included where available.

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1260 FIG. 2. Morphology of the harpetid cephalon.

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1262 FIG. 3. Revised harpetid phylogeny and harpetid families. A: Consensus of 18 most  
1263 parsimonious trees from TNT. B: Bayesian tree from MrBayes. Green: Bremer support  
1264 values, Red: Bootstrap values, Blue: Jackknife values, Black: posterior probabilities  
1265 values.

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1267 FIG. 4. The disparity of the order Harpetida (including reconstructed ancestors) through  
1268 time, with stage level temporal resolution. Red: Sum of variances. Blue: Sum of ranges.  
1269 Minimum number of harpetid genera in relevant time bin. Dashed lines represent major  
1270 mass extinction events.

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1272 FIG. 5. The disparity of the order Harpetida (including reconstructed ancestors) through  
1273 time, with period level temporal resolution. Red: Sum of variances. Blue: Sum of ranges.

1274 Minimum number of harpetid genera in relevant time bin. Dashed lines represent major  
1275 mass extinction events.

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1277 FIG. 6. Phylogenetically corrected harpetid morphospace occupation through time, with  
1278 epoch level resolution.

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1280 FIG. 7. Harpetid morphospace, partitioned by family. Yellow: Harpididae, Green:  
1281 'Entomaspididae', Pink: Heterocaryonidae, Blue: Harpetidae.

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1283 FIG. 8. Harpetid morphospace, partitioned by habitat affinity. Red: shallow water  
1284 affinity. Blue: deep water affinity. Black: generalist. Yellow: Insufficient data.

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1286 TABLE 1. Recognized harpetid genera included or excluded from these analyses.

1287

1288 TABLE 2. PERMANOVA test results of Harpetida, including reconstructed ancestors,  
1289 (Permutation N: 9999, Total sum of squares: 9731,  $F$ : 13.6,  $p$  (same): 0.0001) for  
1290 statistical differences between taxa for each of the four period-level time bins based on  
1291 PCO analyses. Values in regular font are for the Bonferroni corrected  $p$ -values, those in  
1292 italics are the raw  $F$  values.

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1294 TABLE 3. PERMANOVA test results of Harpetida (Permutation N: 9999, Total sum of  
1295 squares: 9105, Within-group sum of squares: 7230,  $F$ : 7.521,  $p$  (same): 0.0001) for  
1296 statistical differences between taxa for each of the four harpetid families based on PCO

1297 analyses. Values in regular font are for the Bonferroni corrected *p*-values, those in italics  
1298 are the raw F values.

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1300 TABLE 4. PERMANOVA test results of Harpetida (Permutation N: 9999, Total sum of  
1301 squares: 3634, Within-group sum of squares: 3397, *F*: 1.603, *p* (same): .003) for

1302 statistical differences between taxa for each of the habitat affinities based on PCO

1303 analyses. Values in regular font are for the Bonferroni corrected *p*-values, those in italics

1304 are the raw F values.

1305 **TABLES**

1306 Table 1: Recognized harpetid genera included or excluded from these analyses.

Genus	Included
<i>Baikadamaspis</i>	Y
<i>Bohemoharpes</i>	Y
<i>Bowmania</i>	Y
<i>Brachyhipposiderus</i>	Y
<i>Chencunia</i>	N
<i>Conococheaguea</i>	Y
<i>Dictyocephalites</i>	N
<i>Dolichoharpes</i>	Y
<i>Dubhglasina</i>	Y
<i>Entomaspis</i>	Y
<i>Eoharpes</i>	Y
<i>Eskoharpes</i>	Y
<i>Globoharpes</i>	Y
<i>Harpes</i>	Y
<i>Harpides</i>	Y
<i>Heterocaryon</i>	Y
<i>Hibbertia</i>	Y
<i>Kathrynia</i>	Y
<i>Kielania</i>	Y
<i>Kitatella</i>	N
<i>Lioharpes</i>	Y
<i>Loganopeltis</i>	Y
<i>Loganopeltoides</i>	Y
<i>Metaharpides</i>	Y
<i>Notchpeakia</i>	Y
<i>Palaeoharpes</i>	N
<i>Paraharpides</i>	Y
<i>Pscemiaspis</i>	Y
<i>Scotoharpes</i>	Y

1331

1332 Table 2: Statistical differences in harpetid morphologies across time.

	Cambrian	Ordovician	Silurian	Devonian
Cambrian	-	16.09	26.03	28.32
Ordovician	0.0006	-	3.613	8.482
Silurian	0.0006	0.0012	-	5.626
Devonian	0.0006	0.0006	0.0006	-

1333

1334 Table 3: Statistical differences in harpetid morphologies across families.

	Entomaspididae	Heterocaryonidae	Harpididae	Harpetidae
Entomaspididae	-	5.195	5.877	4.383
Heterocaryonidae	0.0006	-	12.66	10.42
Harpididae	0.0054	0.0006	-	7.76
Harpetidae	0.0006	0.0006	0.0006	-

1335

1336 Table 4: Statistical differences in harpetid morphologies across habitat affinities.

	<b>Shallow</b>	<b>General</b>	<b>Deep</b> <sub>1337</sub>
<b>Shallow</b>	-	<i>1.944</i>	<i>2.147</i>
<b>General</b>	0.0222	-	<i>1.599</i>
<b>Deep</b>	0.0294	0.246	-



Figure 1: Fossil trilobites of the order Harpetida. A: *Lioharpes venulosus*, B: *Dolichoharpes dentoni* (?), C: *Kielania dorbignyana*, D: *Bohemoharpes ungula*, E: *Scotoharpes spasskii*, F: *Hibbertia wegelini*. 1 cm scale bar included where available.

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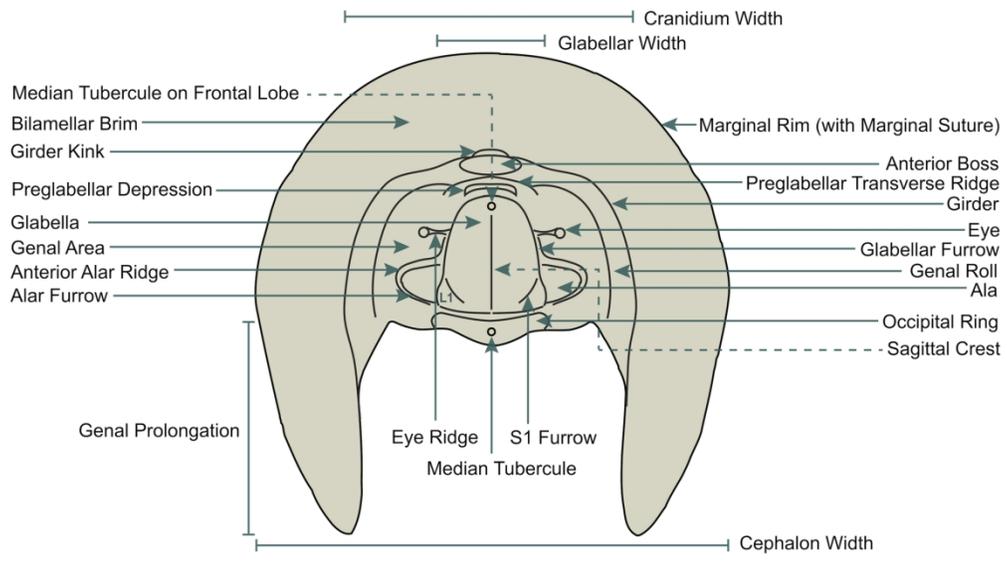


Figure 2: Morphology of the harpetid cephalon.

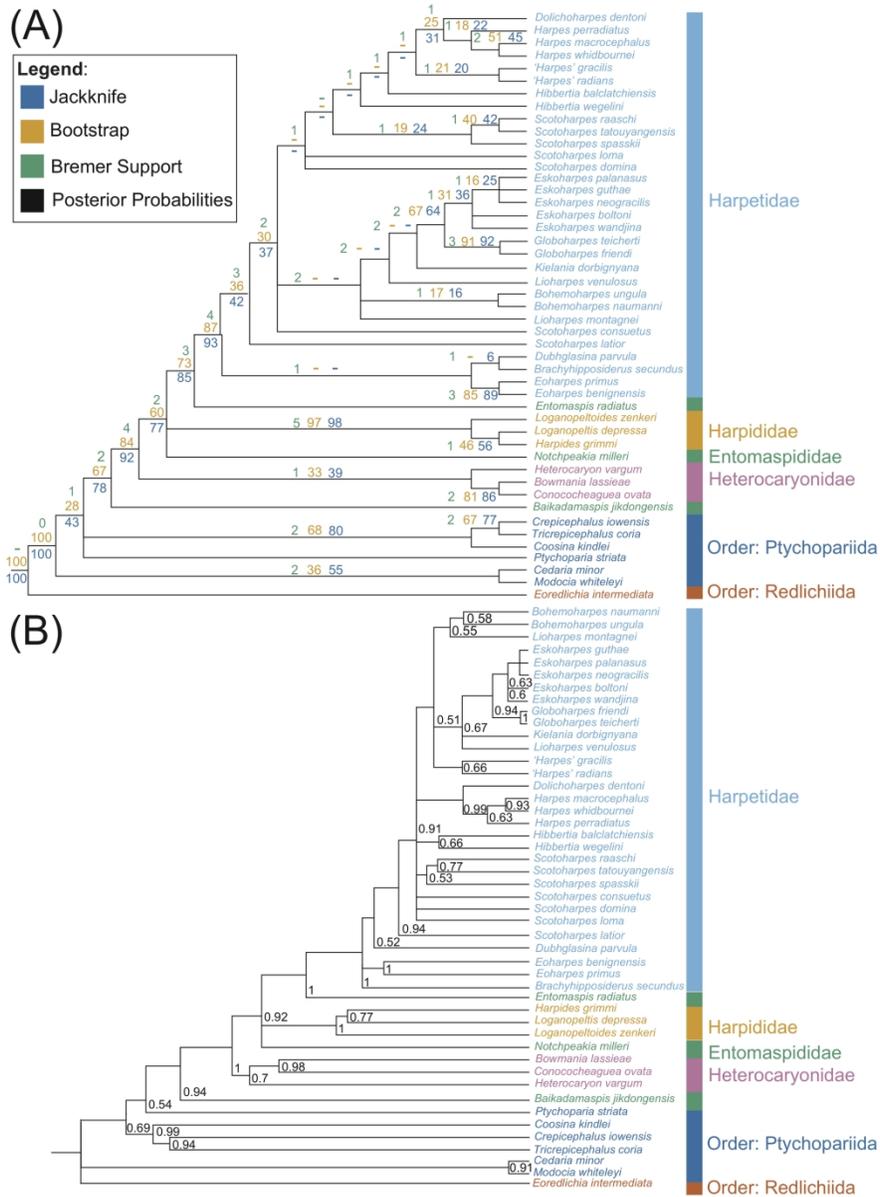


Figure 3: Revised harpetid phylogeny and harpetid families. A: Consensus of 18 most parsimonious trees from TNT. B: Bayesian tree from MrBayes.

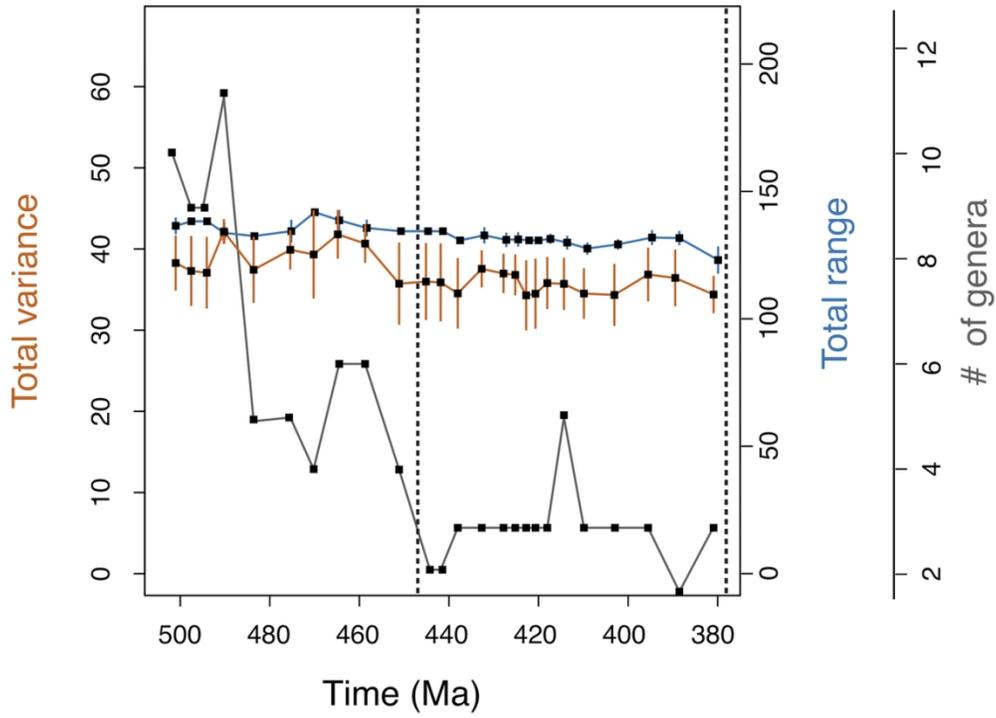


Figure 4: The disparity of the order Harpetida (including reconstructed ancestors) through time, with stage level temporal resolution. Red: Sum of variances. Blue: Sum of ranges. Minimum number of harpetid genera in relevant time bin. Dashed lines represent major mass extinction events.

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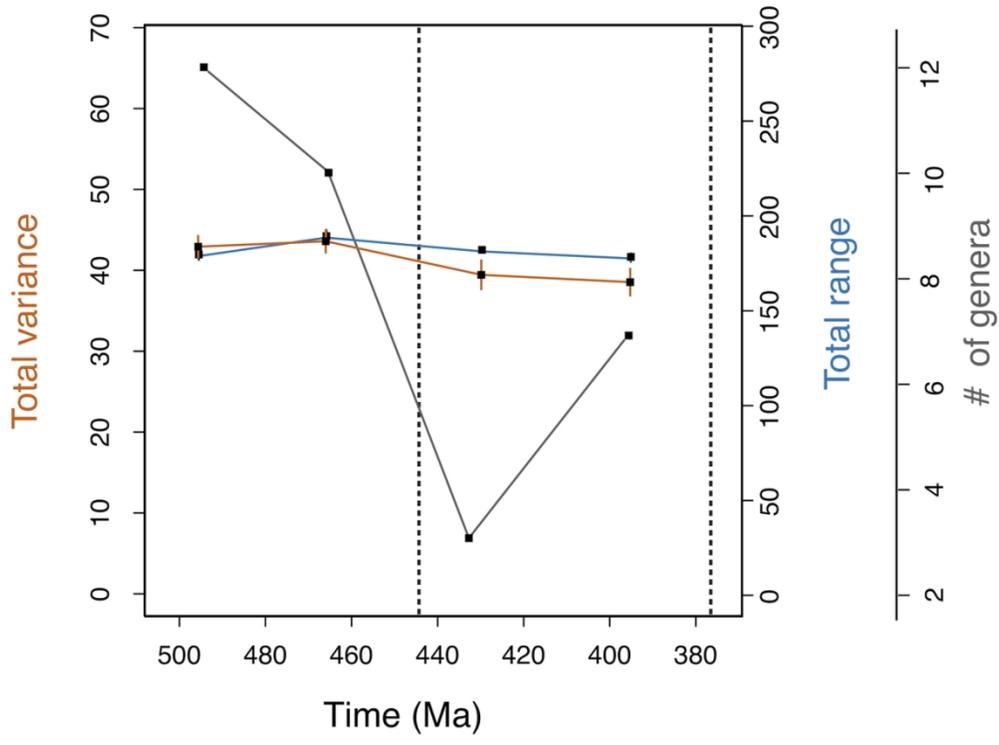


Figure 5: The disparity of the order Harpetida (including reconstructed ancestors) through time, with period level temporal resolution. Red: Sum of variances. Blue: Sum of ranges. Minimum number of harpetid genera in relevant time bin. Dashed lines represent major mass extinction events.

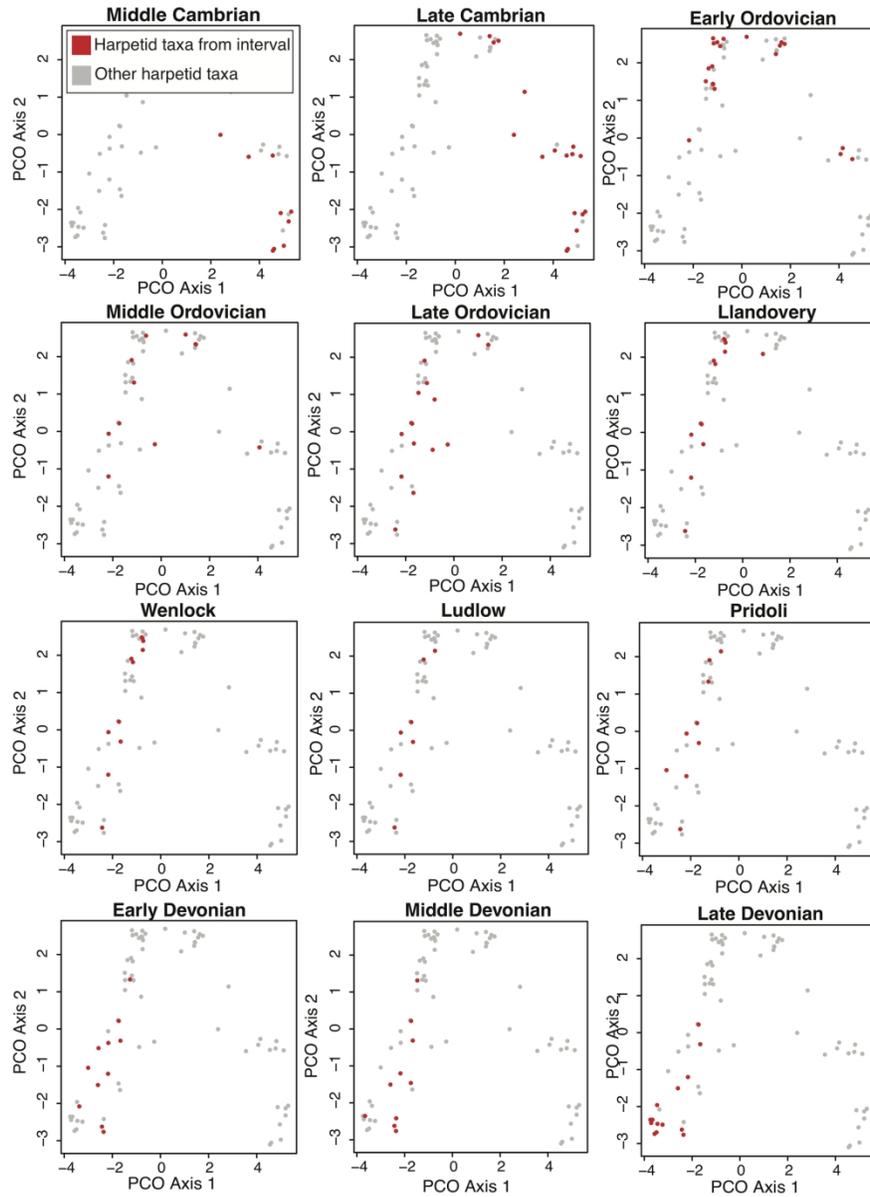


Figure 6: Phylogenetically corrected harpetid morphospace occupation through time, with epoch level resolution.

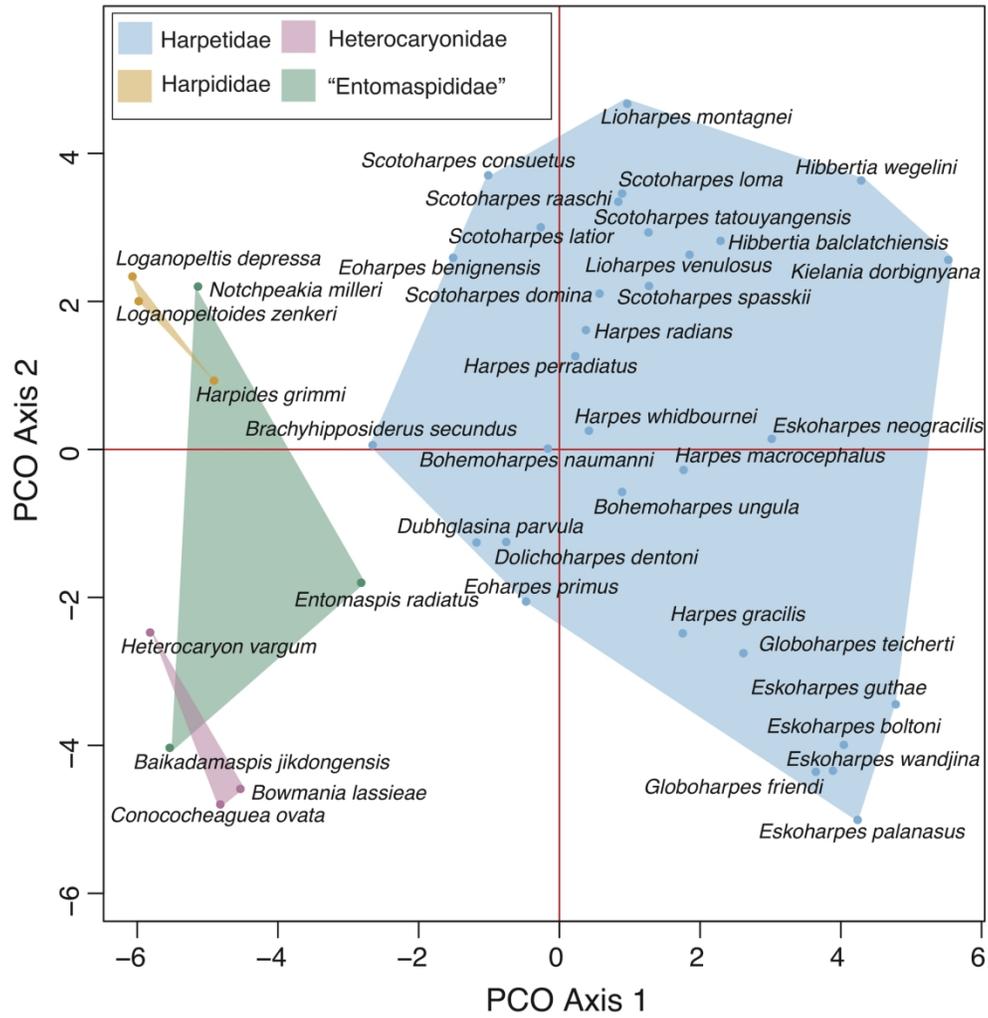


Figure 7: Harpetid morphospace, partitioned by family.

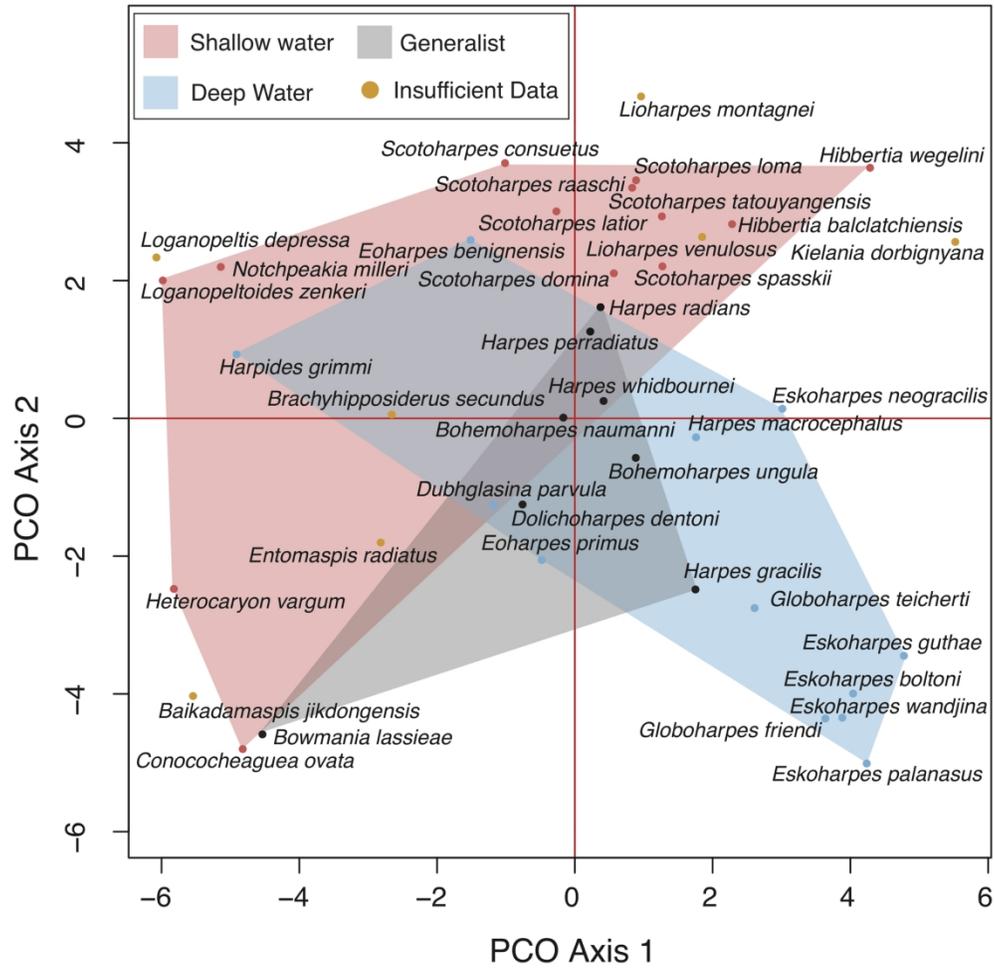


Figure 8: Harpetid morphospace, partitioned by habitat affinity.