




RAPID COMMUNICATION

CONTRASTING PATTERNS OF DISPARITY SUGGEST DIFFERING CONSTRAINTS ON THE EVOLUTION OF TRILOBITE CEPHALIC STRUCTURES DURING THE CAMBRIAN 'EXPLOSION'

by JAMES D. HOLMES* Department of Earth Sciences, Palaeobiology, Uppsala University, Villavägen 16, Uppsala, 752 36, Sweden; james.holmes@geo.uu.se

*Corresponding author

Typescript received 8 June 2022; accepted in revised form 23 December 2022

Abstract: Trilobites are an abundant group of Palaeozoic marine euarthropods that appear abruptly in the fossil record c. 521 million years ago. Quantifying the development of morphological variation (or 'disparity') through time in fossil groups like trilobites is critical in understanding evolutionary radiations such as the Cambrian 'explosion'. Here, I use geometric morphometrics to quantify 'cumulative disparity' in functionally-important structures within the trilobite cephalon across their initial radiation during Cambrian Series 2. Overall cephalic disparity increased rapidly and attained a maximum within several million years. This pattern is dominated by the cephalic outline (in particular the genal spines), reflecting rapid, convergent expansion to the extremes of morphospace in a few early families. In contrast,

removing the outline and focusing on structures such as the glabella and eye ridges (associated with feeding and vision, respectively) showed a more gradual increase in disparity, closer in line with taxonomic diversity and supporting the hypothesis of a relatively accurate trilobite fossil record. These contrasting patterns suggest that disparity in different structures was constrained in different ways, with extrinsic (ecological) factors probably having the major impact on overall disparity. It also implies that patterns of disparity in isolated substructures cannot necessarily be taken individually as representative of overall morphologies.

Key words: geometric morphometrics, trilobite, diversity, evolution, ecology, radiation.

DISPARITY measures the amount of morphological variation within a group of taxa (Hopkins & Gerber 2017) and is often decoupled from taxonomic diversity (e.g. Gould 1991; Foote 1993a, 1997a; Erwin 2007; Hopkins 2013). As such, quantifying how disparity develops (e.g. over the history of a clade or across major extinctions; Guillerme *et al.* 2020; Puttick *et al.* 2020) is important in understanding how different animal groups have evolved through time. Trilobites are an iconic group of biomineralizing Palaeozoic marine euarthropods with an exceptional fossil record, and are often considered a model taxon for examining aspects of early animal evolution (e.g. Paterson *et al.* 2019; Holmes *et al.* 2021a). Previously, broad-scale disparity-through-time analysis using geometric morphometrics has only been conducted for trilobites using cranial outlines, as this allows the comparison of disparate morphologies across their entire history (Foote 1991, 1993a; Hopkins 2014). This study aims to

quantify disparity in higher resolution over a shorter period: specifically Cambrian Series 2, reflecting the initial radiation of trilobites beginning at c. 521 Ma. As such, it incorporates more detailed functional anatomy of the cephalon including the glabella and eye ridges (associated with feeding and vision), and important lateral structures such as the genal spines. The development of disparity is a critical component of evolutionary radiations, and the results presented here show how this occurred in an important early arthropod group during the most iconic of all radiations: the Cambrian 'explosion'.

MATERIAL AND METHOD

The analysis conducted here is restricted to trilobites for which complete dorsal cephalic information is known (including the librigenae of trilobites with dorsal facial

sutures). This makes a standard disparity-through-time analysis problematic, as it is not possible to include a representative sample of taxa in each time bin. However, how a group expands into new areas of morphospace through time can be examined more easily by sampling at a higher taxonomic (e.g. family) level, and using a measure of morphotype generation only (i.e. excluding extinction). Such measures of ‘cumulative disparity’ are rarely used in exploring patterns of disparity as they cannot necessarily tell us about the amount of morphospace occupied at any one time (‘standing disparity’, as noted by Foote 1997a). However, Foote (1997b) used examples of trilobite cumulative disparity to essentially show that although such measures are constrained in certain ways, observed patterns can deviate substantially from random expectations, thus providing information on the development of disparity through time. As such, cumulative disparity can be a useful measure for examining the rate of a clade’s exploration of morphospace across an evolutionary radiation.

The dataset analysed here is based partly on the Cambrian trilobite phylogeny of Paterson *et al.* (2019), as this provides a reasonable sample of well-preserved species at the family level and will allow future integration with this analysis. The majority of Cambrian Series 2 taxa from this dataset were included (eodiscids are a notable exception) and a number of additional taxa were added, in particular some of the earliest trilobites lacking from the original dataset (mostly bigotinids and fallotaspidooids, which represent the majority of taxa present within the first several million years of the trilobite fossil record; Table S1).

As with Paterson *et al.* (2019), species occurrences were dated based on cross-referencing biozones with the calibrated Cambrian timescale of Peng *et al.* (2012) at 0.5 million year increments, in this case with particular reference to the early trilobite biozone correlations of Geyer (2019a), Hollingsworth (2011), Landing *et al.* (2013) and Zhang *et al.* (2017). The full dataset contains 47 species from 22 families ranging in age from c. 521–509 Ma (see Table S1 for a full species list and references) (Holmes 2023). It should be noted that there is some evidence to suggest that the boundary between Cambrian Series 2 and the Miaolingian is potentially considerably younger than the 509 Ma date used here (e.g. Karlstrom *et al.* 2020). However, in this instance relative age is the most important factor, and this will not seriously affect the patterns of disparity observed here. Images of specimens exemplifying the included trilobites species were sourced from the references listed in Table S1, and two-dimensional line reconstructions were created for all species (reconstruction allows information from multiple specimens to be used when single exceptional or articulated specimens are not available). Reconstructions were then digitized with a geometric morphometric approach, using a landmark/semi-landmark configuration devised to

be applicable across the great majority of Cambrian trilobites, and containing information on cephalic outline, glabella and eye ridge morphology (Figs 1, S1). These configurations were then superimposed using generalized Procrustes analysis (GPA), and ‘cumulative disparity’ (the amount of disparity present within and prior to each 0.5 million year time increment) was calculated based on Procrustes variance (equivalent to the ‘sum of variances’, calculated as the trace of the covariance matrix; e.g. Hopkins & Gerber 2017). Separate analyses were conducted both including and excluding the cephalic outline. A separate GPA was conducted for each of the cumulative groups of taxa occurring within and prior to each time increment, although disparity in a single morphospace (i.e. based on a GPA including all taxa) was comparable (Fig. S3). To compare the results with a more random filling of morphospace, 200 replicate samples were created with randomly assigned ages (across the same 0.5 million year time increments) for each of the 47 species, and the resulting means and 95% confidence intervals were plotted against the observed cumulative disparity results. For comparison, cumulative higher-level taxonomic diversity (number of families represented in the dataset) was plotted across the same period. Variation amongst morphologies was visualized using principal components analysis (PCA). All analyses were carried out in the R statistical programming environment (v.4.1.1; R Core Team 2013) using R Studio (v.1.4.1717; RStudio Team 2021). Disparity analysis and GPA were conducted with the R packages geomorph (v.4.0.1; Adams *et al.* 2021; Baken *et al.* 2021) and dispRity (v.1.6.0; Guillerme 2018). For detailed methodology see Appendix S1.

RESULTS

With the cephalic outline included, cumulative disparity increased rapidly (initially in line with a random filling of morphospace) and attained a maximum quickly, followed by a general decrease across the remainder of Cambrian Series 2 (Fig. 1A). This contrasts sharply with a more gradual increase in family-level taxonomic diversity. This pattern implies that the extremes of morphospace were occupied very rapidly by species within a small number of families, followed by consolidation within these bounds across the remainder of Series 2. The majority of shape variation within these configurations reflects genal spine length, with the first axis (PC1) of the PCA plot (Fig. 2A) trending from long genal spines (left) to no genal spines (right), accounting for c. 60% of total variation.

In contrast, by removing the cephalic outline from the analysis and focusing on glabella and eye ridge morphology, the expansion of morphospace is more gradual, increasing more slowly than a random filling of the space,

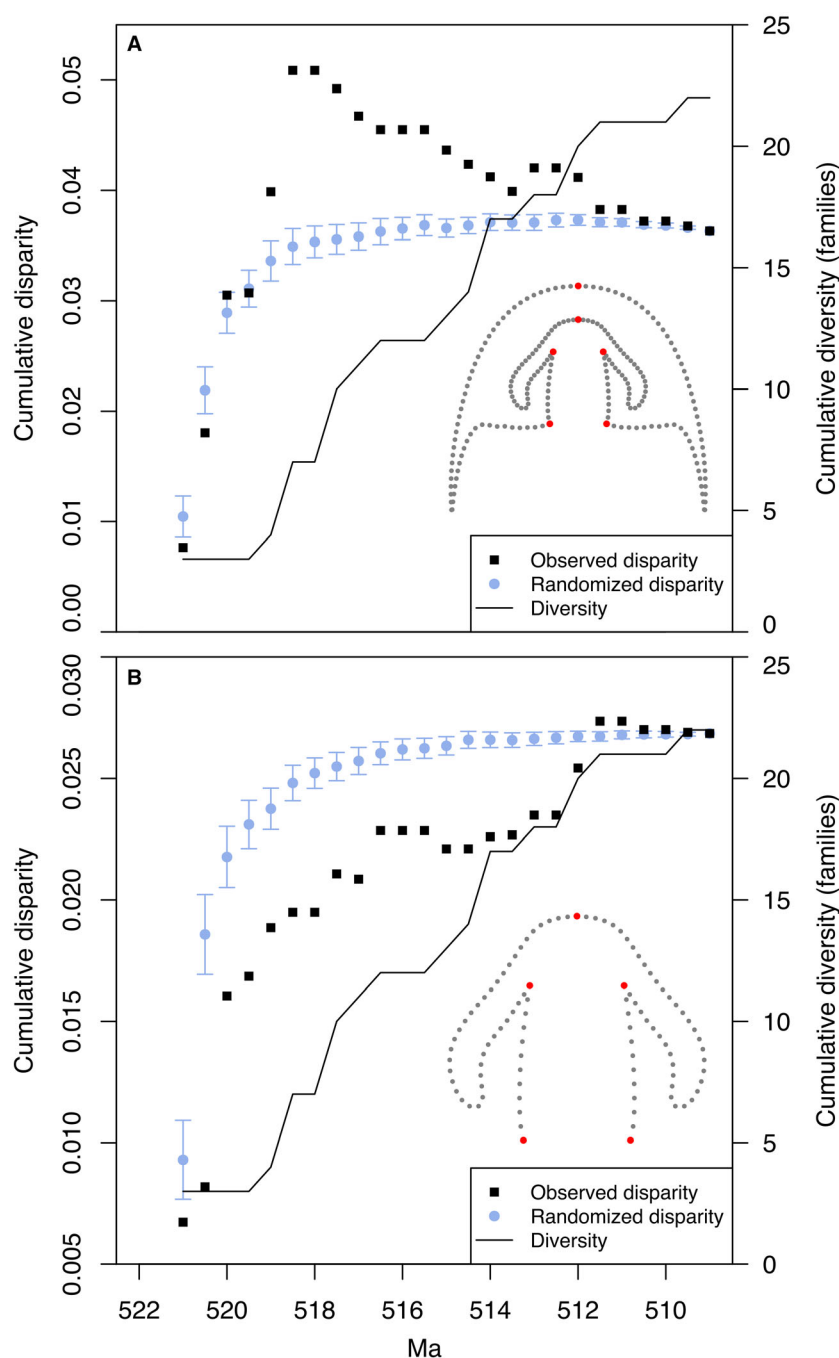


FIG. 1. Cumulative disparity (Procrustes variance) of trilobite cephalic structures across Cambrian Series 2 (*c.* 521–509 Ma): A, including cephalic outline; B, excluding cephalic outline. Analysed configurations are shown with landmarks (red) and sliding semi-landmarks (grey). Black squares indicate observed disparity; light blue circles indicate randomized disparity with 95% confidence intervals. Taxonomic diversity (number of families) is also shown (black line). With the cephalic outline included (A), disparity quickly achieves a maximum and generally decreases thereafter, suggesting rapid filling to the extremes of morphospace. In contrast, with the cephalic outline excluded (B), disparity increases more slowly than a random filling of morphospace, before stabilizing during the middle of Series 2, followed by a second increase associated with a radiation of distinctive olenelloid forms.

and more in line with the increase in taxonomic diversity (Fig. 1B). Initially, disparity increased quickly, before slowing and stabilizing across the middle of Series 2. A

second increase commencing around *c.* 513 Ma reflects a radiation of distinctive olenelloid forms into a new area of morphospace (Fig. 2B).

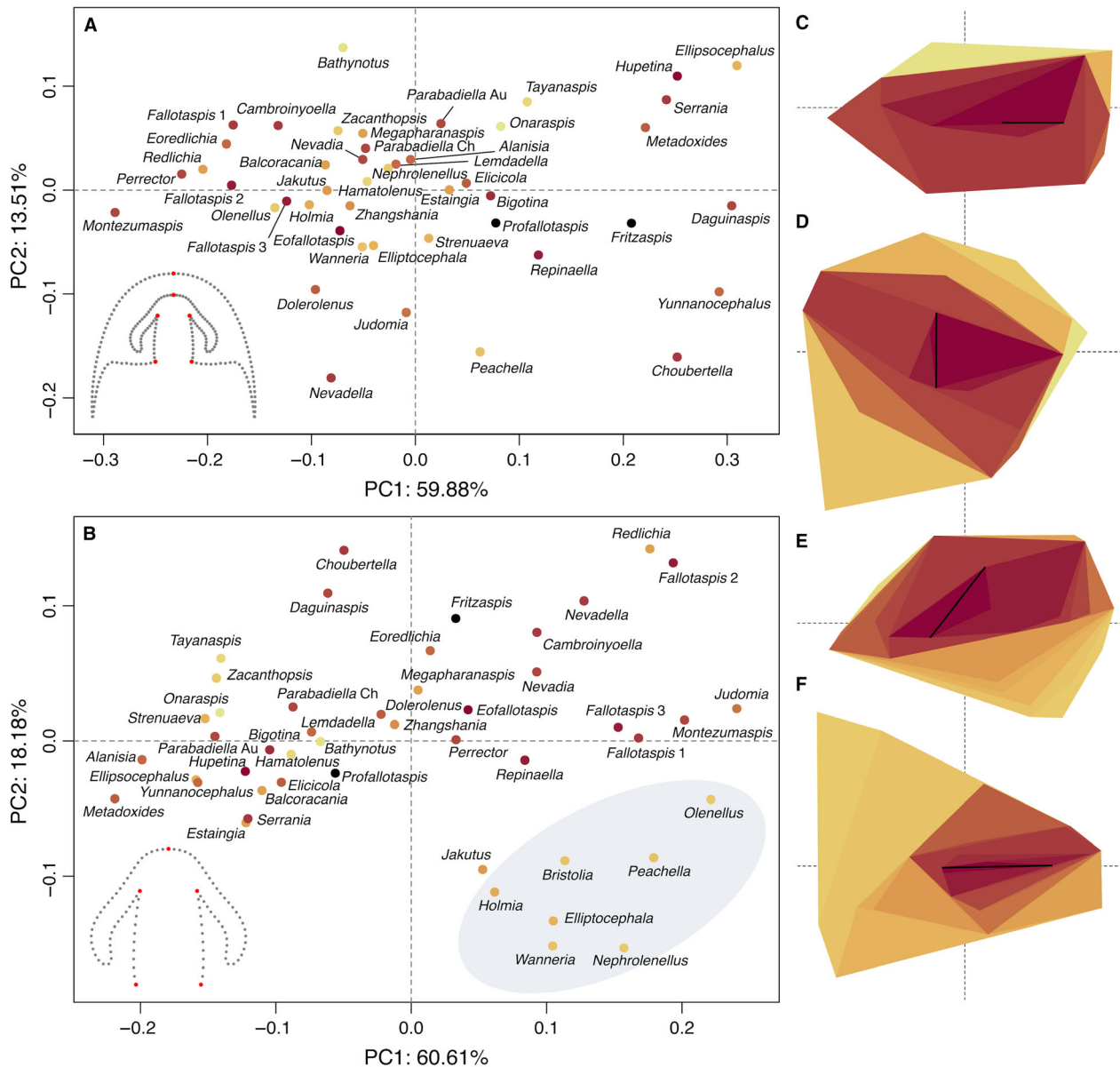


FIG. 2. Principal component analysis (PCA) plots based on generalized Procrustes analysis (GPA) of all analysed taxa, showing their positions in morphospace along the first two principal axes (PC1 and PC2), for configurations: A, including cephalic outline; B, excluding cephalic outline. In A, variation along PC1 (c. 60% of total variation) is dominated by genal spine length, moving from longest genal spines (left, e.g. *Montezumaspis*, *Perrector*) to taxa completely lacking genal spines (right, e.g. *Daguinaspis*, *Ellipsocephalus*). The complete morphospace in A was occupied within a few million years, a result of the rapid adoption of different genal spine morphologies by the earliest trilobites. In contrast, morphospace occupation based solely on glabellar and eye ridge morphologies (B) occurred more slowly across the early part of Cambrian Series 2, followed by a second radiation of olenelloid forms into a new area starting c. 513 Ma (pale oval). PCA convex hulls of time increments for PC1/PC2 (C, E) and PC2/PC3 (D, F) illustrate the differing rates of morphospace expansion: C–D, including the cephalic outline; E–F, excluding the cephalic outline. Colours show relative ages from oldest (darkest/black) to youngest (lightest/pale yellow). As there are only two taxa included at 521 Ma, the hull for this initial increment is invisible; thus, the black lines are provided to show the locations of these taxa. Refer to Table S1 for full species names.

Differences in the rate of morphospace expansion can also be seen in the PCA convex hull plots. When the cephalic outline is included, older taxa (darker hulls and

black lines) rapidly fill the space (Fig. 2C, D), particularly in the PC1/PC2 plot (Fig. 2C), which encompasses the majority of variation (c. 73%). With the outline excluded,

older taxa initially occupy a small area, that more gradually expands outwards as younger taxa (lighter hulls) appear in more distal areas of the space (Fig. 2E, F). The distribution of taxa within the PCA plots (Fig. 2) also shows that, in general, once areas of morphospace became occupied they tended to remain so across Cambrian Series 2, suggesting that cumulative disparity is probably a reasonable estimate of standing disparity across this period.

DISCUSSION

Many studies have shown that disparity is often rapidly established in the early phases of evolutionary radiations, in general outpacing increases in taxonomic diversity and peaking early in the history of clades (see Foote 1997a; Erwin 2007; Hughes *et al.* 2013 and references therein) as is the case for overall trilobite cephalic (cumulative) disparity across Cambrian Series 2 observed here. Such patterns suggest that the development of disparity is constrained in some way, such as by extrinsic (e.g. ecological, physical) or intrinsic (e.g. genetic, developmental) factors (Erwin 2007; Oyston *et al.* 2015). Under this hypothesis, clades rapidly explore available morphospace within these constraints, with subsequent diversification restricted to revisiting or more finely partitioning the intervening space, until the constraints change or evolution can circumvent them (Erwin 2007; Oyston *et al.* 2015). Determining what combination of extrinsic and intrinsic factors might be responsible for constraining patterns of disparity through time is not straightforward (Erwin 2007; Oyston *et al.* 2015). However, post-embryonic development is well known in Cambrian trilobites (e.g. Hou *et al.* 2015; Dai *et al.* 2021; Holmes *et al.* 2021a, 2021b; Hopkins 2021), and can provide insight on the controls of the disparity patterns observed here.

As described above, the rapid increase in overall cephalic disparity is largely related to genal spine morphology. In general, adult (holaspid) early Cambrian trilobites (mostly species within the Order Redlichiida) are restricted to a single pair of genal spines (or in rare examples no spines) extending from the posterolateral corners of the cephalon. Redlichiid genal spines are associated with one of the more anterior conjoined cephalic segments, and in juvenile redlichiids additional pairs of spines are often present; in particular the intergenal spines positioned along the posterolateral margin of the cephalon (Webster 2007, 2015; Dai & Zhang 2012a, 2013; Laibl *et al.* 2017, 2018, 2021). Additional pairs of spines between the genal and intergenal spines (associated with other cephalic segments) are also apparently common in early larval (protaspid) stages of some redlichiids (e.g. in *Redlichia* and *Metaredlichia*) and these are initially very similar to the genal spines (Dai & Zhang 2012b; Zhang & Clarkson 2012; Holmes *et al.* 2021c). As such, there is no obvious

developmental constraint preventing adult redlichiid trilobites from having more than one pair of cephalic spines. In fact, in rare cases multiple pairs of large cephalic spines are known in adult early Cambrian trilobites (e.g. McNamara 1978), probably the result of paedomorphosis (the retention of juvenile features in adult forms), a process suggested to be a major factor in the evolution of novel cephalic morphologies in Cambrian trilobites (McNamara 1986). Therefore, there is presumably some functional or ecological reason why a single pair of large spines is so ubiquitous. The rapid expansion to all extremes of spine length within this limited morphology is probably also related to ecology, reflecting part of an adaptive radiation (or a series of radiations) as trilobites dispersed and evolved to fill a variety of niches across their earliest history. The adoption of biomineralization may represent a potential driver or 'key innovation' (e.g. Simpson 1953; Stroud & Losos 2016) of the rapid and widespread radiation of trilobites, which probably had profound effects on the structure of early marine ecosystems, increasing ecological complexity and creating new niches in the process. This type of niche construction (where opportunities promote radiation that creates additional opportunities, and so on) is most likely to occur when a radiating clade evolves across trophic levels (Schluter 2000; Stroud & Losos 2016), and there is evidence of trilobites predating on other trilobites in the early Cambrian (e.g. Holmes *et al.* 2020; Bicknell *et al.* 2021, 2022). A significant increase in the proportion of trilobites and a corresponding decrease in the number of non-mineralized arthropod taxa in major Lagerstätten across Cambrian Series 2 and the Miaolingian also supports the idea of the increasing ecological success of trilobites (Holmes *et al.* 2018), and biomineralizing arthropods have been important elements of Phanerozoic marine ecosystems ever since. The initial radiation of trilobites was therefore an important factor in the development of ecological complexity across the Cambrian 'explosion'.

In contrast to the overall cephalon, development of disparity in the glabella and eye ridges was more conservative (although still showing an initial rapid increase). Changes in these more proximal structures would require more fundamental reorganization than changes in distal structures such as the genal spines, suggesting that developmental or contingent factors may have played a greater role in constraining the development of disparity in these traits. The expansion into a new area of morphospace at c. 513 Ma by certain olenelloids (in general involving glabellar frontal lobe expansion and eye ridge reduction) suggests some new opportunity and adaptation to a new niche, perhaps involving a different feeding strategy (Fortey & Owens 1999).

The contrasting patterns of disparity in overall and internal cephalic morphology observed here shows that the disparity patterns of some features can swamp those of others. Here, the signal of the cephalic outline overpowers that of the internal structures in the overall analysis, masking

important patterns such as the appearance of the distinctive olenelloid glabella and eye ridge forms starting at *c.* 513 Ma. This finding highlights issues with selecting configurations for, and the subjectivity of, disparity-through-time analyses, and suggests that caution should be exercised when stating that any disparity-through-time pattern of a substructure represents the overall trend for that taxon. For example, the disparity-through-time analyses of Foote (1993a, 1993b) suggested that trilobite disparity peaked in the Ordovician. However, this was based only on cranial outlines and therefore excluded the genal spines and the other important structures considered here. However, by doing so, it also included information on cephalic sutures used in moulting, which are omitted from this analysis (due to many early Cambrian trilobites lacking dorsal sutures). Thus, it is possible that the finding of maximal disparity in the Ordovician is related to a peak in sutural disparity, but not necessarily in, say, overall cephalic disparity (or indeed that of the entire animal). Hopkins (2017) showed that patterns of cranial disparity through time (based on geometric morphometrics) were a reasonable proxy for overall disparity (based on discrete characters) in the trilobite family Pterocephaliidae. Likewise, Foote (1999) showed that disparity in crinoids based on all characters was comparable to that based on cup characters throughout the Phanerozoic; however, overall disparity differed substantially from that based on arm characters. The results presented here confirm that relationships between disparity in different structures and/or substructures can vary in complex ways.

Previously, a cryptic evolutionary history of some length has generally been assumed for trilobites, based largely on the supposed provincialism exhibited by the earliest faunas and the rapid appearance of different groups (e.g. Fortey & Owens 1990; Fortey *et al.* 1996; Lieberman 2003). In fact, the earliest faunas contain a low diversity of probably closely related trilobites (bigotinids and fallotaspidooids), which exhibit only limited provincialism (Holmes & Budd 2022). Regardless, it is important to consider how the presence or absence of a cryptic history might affect the observed development of disparity in the earliest trilobites. Whether or not a cryptic history exists, cumulative disparity will always show some kind of initial increase, given that we are going from a time of no (known) trilobites to one of many. However, if a cryptic history does exist, then we might expect to see groups appear randomly in morphospace as previously invisible lineages appear. The rapid expansion of overall cephalic disparity seen here is initially in line with a more random filling of morphospace. However, this reflects the rapid appearance of a range of genal spine morphologies within groups, rather than the appearance of groups with distinct morphologies; for example, the fallotaspidooids *Fallotaspis* and *Daguinaspis* have very long and no genal spines respectively (Geyer 1996). Thus,

patterns of disparity in a morphospace dominated by this trait show little phylogenetic signal, and cannot inform on the presence of a cryptic history. In contrast, the slower-than-random expansion of glabellar and eye ridge disparity from an initially small area of morphospace is more suggestive of a real diversification event. This hypothesis is supported by the proposal of a close relationship between the earliest (bigotinid and fallotaspidooid) trilobites based on similarities in these structures (Geyer 2019b), and is consistent with the recent suggestion by Holmes and Budd (2022) that trilobites probably arose close to when they appear in the fossil record.

It should also be noted that we can expect trilobites to show rapid diversification early in their history due to survivorship biases such as the push of the past (POTPa; Budd & Mann 2018, 2020). Such effects have generally been overlooked as factors in explaining the rapid establishment of disparity in the early history of clades, although these are likely to have a significant effect. Even though disparity and taxonomic diversity are often decoupled in some way, there is likely to be some correlation between these (at least initially; e.g. Foote 1993a) given that species are generally distinguished by morphological differences. Thus, the higher diversification rate suggested by the POTPa in the early history of successful and long-lived groups like trilobites is likely to correspond to higher rates of morphological evolution across the same period.

CONCLUSION

The results presented here show contrasting patterns of (cumulative) disparity in functionally-important early trilobite cephalic structures across Cambrian Series 2. Overall disparity is dominated by differences in genal spine morphology that reflects rapid, convergent expansion to the extremes of morphospace in a few early families. In contrast, the development of glabellar and eye ridge disparity was more conservative, expanding more slowly from an initially small area of morphospace (reflecting similar morphologies in the earliest trilobites), and supporting the hypothesis of a relatively accurate trilobite fossil record. These contrasting patterns imply that different structures were constrained in different ways, and that caution should be exercised when suggesting disparity patterns of substructures are representative for overall morphologies. Ideally, future studies should adopt a similar strategy to that used here, where the individual patterns of different substructures, and their contributions to overall disparity, can be recognized. This analysis also illustrates that it is possible to reveal trilobite disparity-through-time patterns of functionally-important structures in high resolution using geometric morphometrics. Future work should examine how such patterns vary

across a more comprehensive sample of taxa, in relation to factors such as environment, ecology and phylogeny, to reveal the dynamics of trilobite radiation events.

Acknowledgements. I thank Mike Foote and an anonymous reviewer for insightful comments, Graham Budd and Ben Slater for useful discussions, and Sally Thomas and Javier Álvaro for assistance during the review process.

DATA ARCHIVING STATEMENT

Data files and code for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.tjq2bw2m>

Editor. Javier Álvaro

SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12647>):

Appendix S1. Supplementary text with method details. Includes Figures S1–S3, Table S1 and details of the archived data files.

Fig. S1. Example of line reconstruction and landmark/semi-landmark configurations using *Eofallotaspis tioutensis*.

Fig. S2. Principal component analysis (PCA) plots based on generalized Procrustes analysis (GPA) of all taxa including the cephalic outline: (A) PC1 and PC2, and (B) PC2 and PC3.

Fig. S3. Comparison of cumulative disparity in the same morphospace (containing all taxa) and separate morphospaces as taxa are added at each time bin: (A) including cephalic outline, and (B) excluding cephalic outline.

Table S1. List of trilobite species included in the analysis and references used for dating and obtaining images for reconstructions used in the disparity analyses.

REFERENCES

- ADAMS, D., COLLYER, M., KALIONTZOPOULOU, A. and BAKEN, E. K. 2021. Geomorph: software for geometric morphometric analyses. R package v4.0. <https://cran.r-project.org/package=geomorph>
- BAKEN, E. K., COLLYER, M. L., KALIONTZOPOULOU, A. and ADAMS, D. C. 2021. geomorph v4.0 and gmShiny: enhanced analytics and a new graphical interface for a comprehensive morphometric experience. *Methods in Ecology & Evolution*, **12**, 2355–2363.
- BICKNELL, R. D. C., HOLMES, J. D., EDGECOMBE, G. D., LOSSO, S. R., ORTEGA-HERNÁNDEZ, J., WROE, S. and PATERSON, J. R. 2021. Biomechanical analyses of Cambrian euarthropod limbs reveal their effectiveness in mastication and durophagy. *Proceedings of the Royal Society B*, **288**, 20202075.
- BICKNELL, R. D. C., HOLMES, J. D., PATES, S., GARCÍA-BELLIDO, D. C. and PATERSON, J. R. 2022. Cambrian carnage: trilobite predator–prey interactions in the Emu Bay Shale of South Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **591**, 110877.
- BUDD, G. E. and MANN, R. P. 2018. History is written by the victors: the effect of the push of the past on the fossil record. *Evolution*, **72**, 2276–2291.
- BUDD, G. E. and MANN, R. P. 2020. Survival and selection biases in early animal evolution and a source of systematic overestimation in molecular clocks. *Interface Focus*, **10**, 20190110.
- DAI, T. and ZHANG, X. 2012a. Ontogeny of the trilobite *Estaingia sinensis* (Chang) from the Lower Cambrian of South China. *Bulletin of Geosciences*, **87**, 151–158.
- DAI, T. and ZHANG, X. 2012b. Ontogeny of the redlichiid trilobite *Metaredlichia cylindrica* from the lower Cambrian (Stage 3) of South China. *Journal of Paleontology*, **86**, 646–651.
- DAI, T. and ZHANG, X. 2013. Ontogeny of the redlichiid trilobite *Eoredlichia intermediata* from the Chengjiang Lagerstätte, lower Cambrian, southwest China. *Lethaia*, **46**, 262–273.
- DAI, T., HUGHES, N. C., ZHANG, X. and FUSCO, G. 2021. Absolute axial growth and trunk segmentation in the early Cambrian trilobite *Oryctocarella duyunensis*. *Paleobiology*, **47**, 517–532.
- ERWIN, D. H. 2007. Disparity: morphological pattern and developmental context. *Palaeontology*, **50**, 57–73.
- FOOTE, M. 1991. Morphologic patterns of diversification: examples from trilobites. *Palaeontology*, **34**, 461–485.
- FOOTE, M. 1993a. Discordance and concordance between morphological and taxonomic diversity. *Paleobiology*, **19**, 185–204.
- FOOTE, M. 1993b. Contributions of individual taxa to overall morphological disparity. *Paleobiology*, **19**, 403–419.
- FOOTE, M. 1997a. The evolution of morphological diversity. *Annual Review of Ecology & Systematics*, **28**, 129–152.
- FOOTE, M. 1997b. Sampling, taxonomic description, and our evolving knowledge of morphological diversity. *Paleobiology*, **23**, 181–206.
- FOOTE, M. 1999. Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic crinoids. *Paleobiology*, **25** (suppl. 2), 1–115.
- FORTEY, R. A. and OWENS, R. M. 1990. Evolutionary radiations in the Trilobita. 139–164. In TAYLOR, P. D. and LARWOOD, G. P. (eds) *Major evolutionary radiations*. Clarendon Press.
- FORTEY, R. A. and OWENS, R. M. 1999. Feeding habits in trilobites. *Palaeontology*, **42**, 429–465.
- FORTEY, R. A., BRIGGS, D. E. G. and WILLS, M. A. 1996. The Cambrian evolutionary ‘explosion’: decoupling cladogenesis from morphological disparity. *Biological Journal of the Linnean Society*, **57**, 13–33.
- GEYER, G. 1996. The Moroccan fallotaspide trilobites revisited. *Beringeria*, **18**, 89–199.
- GEYER, G. 2019a. A comprehensive Cambrian correlation chart. *Episodes Journal of International Geoscience*, **42**, 321–332.

- GEYER, G. 2019b. The earliest known West Gondwanan trilobites from the Anti-Atlas of Morocco, with a revision of the Family Bigotinidae Hupé, 1953. *Fossils & Strata*, **64**, 55–153.
- GOULD, S. J. 1991. The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiology*, **17**, 411–423.
- GUILLEMERME, T. 2018. dispRity: a modular R package for measuring disparity. *Methods in Ecology & Evolution*, **9**, 1755–1763.
- GUILLEMERME, T., COOPER, N., BRUSATTE, S. L., DAVIS, K. E., JACKSON, A. L., GERBER, S., GOSWAMI, A., HEALY, K., HOPKINS, M. J., JONES, M. E. H., LLOYD, G. T., O'REILLY, J. E., PATE, A., PUTTICK, M. N., RAYFIELD, E. J., SAUPE, E. E., SHERRATT, E., SLATER, G. J., WEISBECKER, V., THOMAS, G. H. and DONOGHUE, P. C. J. 2020. Disparities in the analysis of morphological disparity. *Biology Letters*, **16**, 20200199.
- HOLLINGSWORTH, J. S. 2011. Lithostratigraphy and biostratigraphy of Cambrian Stage 3 in western Nevada and eastern California. *Museum of Northern Arizona Bulletin*, **67**, 26–42.
- HOLMES, J. D. 2023. Data from: Contrasting patterns of disparity suggest differing constraints on the evolution of trilobite cephalic structures during the Cambrian 'explosion'. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.tqjq2bw2m>
- HOLMES, J. D. and BUDD, G. E. 2022. Reassessing a cryptic history of early trilobite evolution. *Communications Biology*, **5**, 1177.
- HOLMES, J. D., GARCÍA-BELLIDO, D. C. and LEE, M. S. Y. 2018. Comparisons between Cambrian Lagerstätten assemblages using multivariate, parsimony and Bayesian methods. *Gondwana Research*, **55**, 30–41.
- HOLMES, J. D., PATERSON, J. R. and GARCÍA-BELLIDO, D. C. 2020. The trilobite *Redlichia* from the lower Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia: systematics, ontogeny and soft-part anatomy. *Journal of Systematic Palaeontology*, **18**, 295–334.
- HOLMES, J. D., PATERSON, J. R. and GARCÍA-BELLIDO, D. C. 2021a. Complex axial growth patterns in an early Cambrian trilobite from South Australia. *Proceedings of the Royal Society B*, **288**, 20212131.
- HOLMES, J. D., PATERSON, J. R. and GARCÍA-BELLIDO, D. C. 2021b. The post-embryonic ontogeny of the early Cambrian trilobite *Estaingia bilobata* from South Australia: trunk development and phylogenetic implications. *Papers in Palaeontology*, **7**, 931–950.
- HOLMES, J. D., PATERSON, J. R., JAGO, J. B. and GARCÍA-BELLIDO, D. 2021c. Ontogeny of the trilobite *Redlichia* from the lower Cambrian (Series 2, Stage 4) Ramsay Limestone of South Australia. *Geological Magazine*, **158**, 1209–1223.
- HOPKINS, M. J. 2013. Decoupling of taxonomic diversity and morphological disparity during decline of the Cambrian trilobite family Pterocephaliidae. *Journal of Evolutionary Biology*, **26**, 1665–1676.
- HOPKINS, M. J. 2014. The environmental structure of trilobite morphological disparity. *Paleobiology*, **40**, 352–373.
- HOPKINS, M. J. 2017. How well does a part represent the whole? A comparison of cranial shape evolution with exoskeletal character evolution in the trilobite family Pterocephaliidae. *Palaeontology*, **60**, 309–318.
- HOPKINS, M. J. 2021. Ontogeny of the trilobite *Elrathia kingii* (Meek) and comparison of growth rates between *Elrathia kingii* and *Aulacopleura koninckii* (Barrande). *Papers in Palaeontology*, **7**, 985–1002.
- HOPKINS, M. J. and GERBER, S. 2017. Morphological disparity. 965–976. In NUNO DE LA ROSA, L. and MÜLLER, G. (eds) *Evolutionary developmental biology: A reference guide*. Springer.
- HOU, J., HUGHES, N. C., LAN, T., YANG, J. and ZHANG, X.-G. 2015. Early postembryonic to mature ontogeny of the oryctocephalid trilobite *Duodingia duodingensis* from the lower Cambrian (Series 2) of southern China. *Papers in Palaeontology*, **1**, 497–513.
- HUGHES, M., GERBER, S. and WILLS, M. A. 2013. Clades reach highest morphological disparity early in their evolution. *Proceedings of the National Academy of Sciences*, **110**, 13875–13879.
- KARLSTROM, K. E., MOHR, M. T., SCHMITZ, M. D., SUNDBERG, F. A., ROWLAND, S. M., BLAKEY, R., FOSTER, J. R., CROSSEY, L. J., DEHLER, C. M. and HAGADORN, J. W. 2020. Redefining the Tonto Group of Grand Canyon and recalibrating the Cambrian time scale. *Geology*, **48**, 425–430.
- LAIBL, L., ESTEVE, J. and FATKA, O. 2017. Giant post-embryonic stages of *Hydrocephalus* and *Eccaparadoxides* and the origin of lecithotrophy in Cambrian trilobites. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **470**, 109–115.
- LAIBL, L., CEDERSTRÖM, P. and AHLBERG, P. 2018. Early post-embryonic development in *Ellipsostrenua* (Trilobita, Cambrian, Sweden) and the developmental patterns in Ellipsocphaloidea. *Journal of Paleontology*, **92**, 1018–1027.
- LAIBL, L., MALETZ, J. and OLSCHESKI, P. 2021. Post-embryonic development of *Fritzenellus* suggests the ancestral morphology of the early developmental stages in Trilobita. *Papers in Palaeontology*, **7**, 839–859.
- LANDING, E., GEYER, G., BRASIER, M. D. and BOWRING, S. A. 2013. Cambrian evolutionary radiation: context, correlation, and chronostratigraphy—overcoming deficiencies of the first appearance datum (FAD) concept. *Earth-Science Reviews*, **123**, 133–172.
- LIEBERMAN, B. S. 2003. Taking the pulse of the Cambrian radiation. *Integrative & Comparative Biology*, **43**, 229–237.
- McNAMARA, K. J. 1978. Paedomorphosis in Scottish olenellid trilobites (early Cambrian). *Palaeontology*, **21**, 635–655.
- McNAMARA, K. J. 1986. The role of heterochrony in the evolution of Cambrian trilobites. *Biological Reviews*, **61**, 121–156.
- OYSTON, J. W., HUGHES, M., WAGNER, P. J., GERBER, S. and WILLS, M. A. 2015. What limits the morphological disparity of clades? *Interface Focus*, **5**, 20150042.

- PATERSON, J. R., EDGECOMBE, G. D. and LEE, M. S. Y. 2019. Trilobite evolutionary rates constrain the duration of the Cambrian explosion. *Proceedings of the National Academy of Sciences*, **116**, 4394–4399.
- PENG, S., BABCOCK, L. E. and COOPER, R. A. 2012. The Cambrian period. 437–488. In GRADSTEIN, F. M., OGG, J. G., SCHMITZ, M. D. and OGG, G. M. (eds) *The geologic time scale 2012*, Vol. 2. Elsevier.
- PUTTICK, M. N., GUILLERME, T. and WILLS, M. A. 2020. The complex effects of mass extinctions on morphological disparity. *Evolution*, **74**, 2207–2220.
- R CORE TEAM. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- RSTUDIO TEAM. 2021. RStudio: Integrated development environment for R. RStudio, PBC, Boston, MA. <http://www.rstudio.com/>
- SCHLUTER, D. 2000. *The ecology of adaptive radiation*. Oxford University Press, 288 pp.
- SIMPSON, G. G. 1953. *The major features of evolution*. Columbia University Press, 434 pp.
- STROUD, J. T. and LOSOS, J. B. 2016. Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, & Systematics*, **47**, 507–532.
- WEBSTER, M. 2007. Ontogeny and evolution of the early Cambrian trilobite genus *Nephrolenellus* (Olenelloidea). *Journal of Paleontology*, **81**, 1168–1193.
- WEBSTER, M. 2015. Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*, with implications for olenelline phylogeny and macroevolutionary trends in phenotypic canalization. *Journal of Systematic Palaeontology*, **13**, 1–74.
- ZHANG, X.-G. and CLARKSON, E. N. K. 2012. Phosphatized eodiscoid trilobites from the Cambrian of China. *Palaeontographia Abteilung A*, **297**, 1–121.
- ZHANG, X., AHLBERG, P., BABCOCK, L. E., CHOI, D. K., GEYER, G., GOZALO, R., STEWART HOLLINGSWORTH, J., LI, G., NAIMARK, E. B., PEGEL, T., STEINER, M., WOTTE, T. and ZHANG, Z. 2017. Challenges in defining the base of Cambrian Series 2 and Stage 3. *Earth-Science Reviews*, **172**, 124–139.