

Supplementary Material

Permian trilobites and the applicability of the “living fossil” concept to extinct clades

Melanie J. Hopkins*, Peter J. Wagner, Katherine J. Jordan

* Correspondence: Melanie J. Hopkins: mhopkins@amnh.org

1 Supplementary Information on Materials and Methods

Basic trilobite skeletal anatomy

The mature trilobite exoskeleton is divided primarily between the cephalon (head shield) and the trunk (Supplementary Figure 2). The cephalon was comprised of several sclerites, including the cranidium and librigena, which are articulated along sutures that separate during ecdysis. Two prominent features of the cephalon include the glabella, which is the axial region of the cephalon, and the palpebral lobes, which overlie the eye surface in species which had compound eyes. The trunk had two regions: the thorax which was comprised of disarticulated thoracic tergites (traditionally called thoracic segments) and the pygidium (tail shield).

Morphometric analysis of the trilobite head

Preparation and biases in the datasets used to describe head shield (cranidium/cephalon) shape.

The Foote (1993) dataset consists of outline data describing the shape of the cranidium, or the medial sclerite of the head shield (Supplementary Figure 2), which were then subjected to Fourier analysis (Foote, 1989; 1991). For this study, we used the dataset of Fourier coefficients (available at http://geosci.uchicago.edu/~foote/MORPHDAT/TRILOBITE_DATA.TXT). The dataset was treated as described in Hopkins (2014) with the following additional modifications: 1) duplicate examples of species were removed randomly (some species are represented by more than one specimen in the original dataset) and all species identified only to “sp” were removed if their genus was represented by congenetics identified to species level (for example, data for specimen BMN220, identified as *Ampyx sp.* from Laurentia, was removed because there is a sampled specimen of *Ampyx virginensis*, also Laurentian, among others); 3) all agnostoids and eodiscids (N = 12) were removed. The resulting dataset has 700 specimens (reduced from N = 1123) and is available in Supplementary Dataset 1. This dataset is heavily biased by taxa sampled from Laurentian North America (N = 552, or 78% of the dataset). 81 families are represented; the median number of species per family is 6. The Proetidae is the most heavily sampled family with a sample size of 58 (8.3% of the total dataset).

The Suárez and Esteve (2021) dataset consists of semi-landmarks describing the shape of the cephalon (Supplementary Figure 2). For this study, we used the dataset of Procrustes coordinates, which was modified as follows: 1) species assigned to Phillipsiidae were included within

Proetidae; 2) because there were only 3 specimens sampled from the Lower Silurian, they were combined with the taxa sampled from the Middle Silurian; and 3) because there were only 2 specimens sampled from the Upper Carboniferous, they were combined with taxa sampled from the Lower Carboniferous. In addition, the following specimens were removed: 1) all agnostoids (N = 10); 2) all taxa with uncertain placement in geologic series (N = 4); and 3) duplicate examples of species, randomly selected (N = 4). The resulting dataset has 382 specimens (reduced from 400) and is available in Supplementary Dataset 1. Original sampling for this dataset was biased towards species for which enrolment behavior type can be classified. 66 families are represented; the median number of species per family is 3. The Proetidae is the most heavily sampled family with a sample size of 55 (13.8% of the total dataset).

Analyses of the head shield datasets

Each dataset described above was subjected to a principal components analysis. Disparity was measured using sum of ranges, which describes the breadth of morphospace occupation, and sum of variances, which describes the density of taxon distribution in morphospace (Hopkins and Gerber, 2017; Guillaume et al., 2020). Disparity indices were calculated across all principal component scores for subsets of the data, including for each family and within each time interval. In order to see what the disparity estimates for Proetidae may have been at more common sample sizes, the subset of data for that family was randomly resampled 1000 times at the median sample size across families (N = 6 for the Foote dataset; N = 3 for the Suárez and Esteve dataset). In order to determine if the morphological change was significant through time, we ran an np-MANOVA (Collyer et al., 2014) using the R package rpp (Collyer and Adams, 2018). We applied the np-MANOVA to both the entire dataset and to just the Proetidae. Results are shown in Supplementary Table 1. See Supplementary Dataset 1 for annotated R script.

Morphological analysis of the entire exoskeleton

Our taxon sampling scheme, character design, and analysis were designed for the specific purpose of characterizing the common conception of the basic or typical trilobite body form, and the extent to which different trilobite clades adhered to that conception as well as the extent to which character combinations expressed by Permian trilobites could be considered “ancestral”. To accomplish this, we compare Permian members of the Proetida to earlier members of all trilobite orders currently considered valid in the Paleobiology Database (PBDB). The PBDB classification itself largely reflects Whittington et al. (1997), but with more recent emendations by Whittington (2002; 2009), Adrain (2011), Bignon et al. (2020) and others. We use orders for this basic aspect of comparison because we assume that concepts around “living fossils” revolve around the sorts of general features that typify higher taxa such as orders.

Taxon sampling

We used the Paleobiology Database (PBDB) to draw up a list of the most common trilobite genera within each order within each geologic period (Supplementary Dataset 2). The PBDB currently treats nearly 3500 trilobite genera and subgenera as valid taxa. This obviously represents far more taxa than we could analyze. Moreover, we think it probable that concepts about “living fossils”

revolve around relatively common fossil taxa. Therefore, we use the most common genera from each order from each period to establish the range of anatomical forms among genera extinct present before the Permian. Genera were sampled based on the average ranking based on two metrics:

- 1) numbers of species-level occurrences; and,
- 2) numbers of rock-units that those occurrences occupy.

We use occurrence numbers because this is strongly correlated with *occupancy*, i.e., the number of areas occupied by a taxon (Liow, 2013) and occupancy is a common macroecological metric for commonness (e.g., Brown, 1984). However, non-random sampling can greatly inflate the numbers of occurrences for trilobites from well-sampled rock-units. This sometimes reflect monographic effects (sensu Raup and Boyajian, 1988), in which major works provide dozens of localities from restricted areas. However, even without monographic effects, “binge sampling” of particularly fossiliferous rock units can result in numerous papers reporting the occurrences of common species from those rocks (Wagner et al., 2018). Using numbers of rock-units mitigates both monographic effects and binge sampling by requiring that members of a genus be found in multiple areas and/or multiple environmental types to be considered common. This also comes closer to satisfying macroecological definitions of “high occupancy” taxa that are found in numerous areas and environments (Hurlbert and White, 2007). The only trilobite order that was not sampled in this process was the Order Harpetida, which currently consists of 46 genera (Beech and Lamsdell, 2021), only 21 of which have entries in the PBDB. Data were downloaded from the Paleobiology Database on 25 September 2022 and RData files and R scripts are archived in Supplementary Dataset 3.

We restricted coding to those taxa that have both the cephalon (“head”) and pygidium (“tail”) preserved. Although “completeness” in the fossil record often refers to taxon-sampling alone (e.g., Foote and Raup, 1996), another aspect of completeness is the proportion of the skeleton that is sampled (Dunhill et al., 2012; Benton et al., 2013). Although well-sampled taxa obviously have a higher chance of providing complete skeletons, trilobites do provide exceptions where commonly-sampled genera are known exclusively from only one sclerite (either the cranidium or the pygidium). Common taxa of this sort included *Gaoloupingia* Yuan and Yin, 1998, *Perunaspis* Přibyl, 1949, *Jegorovaia* Lu, 1964, *Camaraspis* Ulrich and Resser, in Ulrich 1924, and *Joshuaspis* Choi et al, 2008. In one case, we had to exclude a genus because the relevant literature was unavailable to us (*Aplexura* Rosova, 1963). Most of those excluded were low ranking in our list and are commonly found in regions where most fossils are documented in older works from China or the former Soviet Union. With the exception of Cambrian trinucleides, all sampled orders in each period were represented by a minimum of five genera and maximum of seven genera.

Seven taxa in the list are subgenera and many of the other taxa were originally described as subgenera that have subsequently been elevated to genera. Because of this tendency in practice (and its codification through the publication of Jell and Adrain [2002]), we also treated each listed subgenus as an operational taxonomic unit (OTU) separate from the rest of the genus and restricted our coding of the latter. For example, *Proceratopyge* Wallerius, 1895, and *Proceratopyge* (*Sinoproceratopyge*) Lu and Lin, 1980, are both listed and we restricted coding for the former to species assigned to *Proceratopyge* (*Proceratopyge*). The only exception to this is *Olenellus* Hall, in Billings 1861, for which we based coding on species of both *Olenellus* (*Olenellus*) and *Olenellus*

(*Paedeumius*) Walcott, 1910, because phylogenetic analysis questions their separability as monophyletic groups and thus *Paedeumius* species have been retained within *Olenellus* despite the recombination of many “*Olenellus*” species to other genera (Lieberman, 1999), which happen to also be represented in our PBDB query (for example, *Mesonacis* Walcott, 1885, *Bristolia* Harrington, 1956). We also restricted the coding for each genus to the species that occurred within the period for which that genus was sampled. Thus for genera which were sampled from more than one geologic period, each was treated as a separate OTU.

In the PBDB, familial assignments of genera are based primarily on Jell and Adrain (2002) as well as subsequent literature; we checked these assignments and updated any that were out-of-date. There are currently two primary competing taxonomies placing families in orders, that of Fortey (1997) and that of Adrain (2011). These taxonomies largely or completely agree on familial assignments to the following orders: Redlichiida Richter, 1932, Phacopida Salter, 1864, Corynexochida Kobayashi, 1935, and Asaphida Salter, 1864. The primary differences between the taxonomies include: 1) Fortey (1997) included the odontopleurids in Order Lichida Moore, in Harrington 1959, but Adrain (2011) assigned them to Order Odontopleurida Whittington, in Harrington 1959; 2) Adrain (2011) argued that Order Ptychopariida Swinnerton, 1915, should be abandoned entirely and moved some families into a newly created Order Olenida; 3) Adrain (2011) proposed that Order Proetida Fortey and Owens, 1975, should be reduced to two families, the Proetidae Salter, 1864, and Tropidocoryphidae Přibyl, 1946, and placed other families assigned to Proetida by Fortey (1997) in a newly created Order Aulacopleurida. A subsequent phylogenetic analysis by Lamsdell and Selden (2015) refuted the Adrain (2011) conception of Order Aulacopleurida in favor of Fortey (1997). The PBDB reflects this history in maintaining Order Ptychopariida and Order Proetida sensu Fortey (1997) but accepting Order Odontopleurida and Order Olenida following Adrain (2011). The current taxonomy in the PBDB also includes the Order Trinucleida Swinnerton, 1915 (Bignon et al., 2020), comprised of families formerly assigned to the superfamily Trinucleoidea Hawle and Corda, 1847, and placed within the Order Asaphida in both the Fortey (1997) and Adrain (2011) taxonomies. For the purposes of this analysis, we followed the taxonomy in the PBDB.

One obvious concern is that commonly occurring genera might represent taxonomic “wastebaskets” and thus their morphologies might not represent what is actually commonly sampled. In general, common genera in the fossil record tend to share properties suggesting that they do not simply represent wastebaskets (Plotnick and Wagner, 2018; Wagner et al., 2018). Nevertheless, we did add over 200 taxonomic records and over 900 taxonomic opinions into the PBDB in support of this project in order to refine the definitions of many of the genera used in this study.

Character matrix

We created 37 characters that describe notable or unusual exoskeletal morphologies that might be considered uncommon or not typical of a generic trilobite body plan. Each character has the form of “Do any species have...”. Each character was assigned two states, one that indicated that no congeneric species showed the described morphological feature (0) or that at least some of the congeneric species showed the described morphological feature (1). Some characters are logically

dependent on the presence of an anatomical character. For example, the character “Do any species have stalked eyes?” is dependent on the presence of eyes. For genera where all observed species lacked eyes, but we remain unsure if ALL species lacked eyes, we coded this character as “?”. In the instance where we had some certainty that ALL species lacked the feature in question, we coded this character as inapplicable (“—”). We also used the “?” token for characters which we could not code because of missing data (for example, if the thorax was unknown for all observed species, we were unable to determine if any species had macropleural spines on the thorax).

Although it may seem subjective, this method of character selection is just as rigorous as more standard character selection for disparity or phylogenetic analysis, in that the process is suited to the purpose of the study and necessarily seeks a finite number of descriptions of morphology that are believed to be informative to that purpose. Because living fossil concepts are based on general features, we chose characters that describe traits not expressed by species with “generic” body plans (for example, *Elrathia kingii* (Meek, 1870), Supplementary Figure 2). We also sought characters that were easily identifiable. These traits -- or a particular expression of the traits -- may characterize groups, but their presence is not necessarily limited to those groups. For example:

Character 1: Do any species have macropleural spines on the thorax? Macropleural spines are spines that extend from the pleural (outside) ends of one thoracic tergite in the thorax. The rest of the thorax has either short or no pleural spines. The tergite which bears the macropleural spine may be, but is not necessarily, wider sagittally than other thoracic tergites. Species with equally long spines extending from many or all thorac segments would not be considered to have macropleural spines. Examples of species with macropleural spines include *Shumardia (Conophrys) salopenesis* (Fortey and Owens, 1991, fig. 8n) and *Olenellus (Paedeumius) transitans* (Palmer and Repina, 1993, fig. 3.3).

Some characters describe increased complexity within a category of trait. For example:

Character 15: Do any species have complex surface sculpture on the dorsal exoskeleton? Here we defined a threshold for considering sculpture to be complex or not. Small, evenly-distributed granulation or pitting is considered "simple" sculpture whereas reticulate sculpture, organized tubercles/granulation/spines, fingerprint patterns, and irregularly shaped granulation is considered "complex." *Aponileus laikaae* (Adrain et al., 2012, Plate 3) is an example of complex sculpture.

Some characters are structured to capture anything besides the generic expression of the trait. For example:

Character 32: Do any species have anything but a semi-circular pygidium? This character focuses on the overall shape of the lateral and posterior margin of the pygidium and how smoothly curved it is, disregarding small indentations at the sagittal axis or spines. This sort of trait can be difficult to code consistently, but no more so than categorical characters describing pygidial shape that have been used for phylogenetic analysis (for example, “semi-circular” vs “triangular” vs “subquadrate”).

Supplementary Dataset 4 contains character descriptions and codings as well as observed species and literature consulted for each genus. The matrix also includes notes to prevent conflation of characters where this might have been a problem. For example:

Character 31: Do any species have complex structures at the anterior part of the cephalon? Examples of such structures include pits within the anterior border furrow (e.g., *Cernuolimbus arcticus*, Hopkins, 2011, fig. 1.5) or fenestra (e.g., *Odontocephalus aegeria*, Whiteley et al, 2002, Plate 123). Taxa with fringed cephalon (Character 10) may have pitting that extends to the anterior part of cephalon, but would only be coded positively for this character (Character 31) if the expression at the anterior part is different from the rest of the fringe (e.g., *Dionide magnifica*, Owen and Bruton, 1980, Plate 6, fig. 1).

Readers may notice that species of *Proetus* Steininger, 1831, the type genus for the family Proetidae, did not express any of the unusual traits described by the 37 characters. As we did not use *Proetus* as a model for developing the characters, this was a natural outcome of the data collection process. There are also two other genera (*Olenaspella* Wilson, 1956, and *Niobe* (*Niobella*) (Reed, 1931)) from different orders where no species were observed to express any of the unusual traits.

18% of the taxa were coded for only the cephalon and pygidium (thorax unknown in observed species). In the interest of avoiding large amounts of missing information, we did not include any characters describing the ventral morphology. Similarly, we also excluded characters describing the non-skeletal anatomy of trilobites, such as appendages. Interestingly there appears to be much less variation in soft-body anatomy than there is in the exoskeleton of trilobites, even as ongoing discoveries plus the application of new imaging technologies continue to expand our knowledge of variation in appendages, including in the position of setae for grooming (Hou et al., 2023), the shape of gill filaments (Hou et al., 2021; Siveter et al., 2021), the relative size of branches and podites across species (Ramsköld and Edgecombe, 1996; Holmes et al., 2020; Hou et al., 2021), and the relative size of appendages within species (Pérez-Peris et al., 2021; Losso and Ortega-Hernández, 2022). It is possible that our understanding of appendage variation is biased by the fact that only a fraction of known species have soft-tissue remains (e.g., Hughes, 2003; Lerosey-Aubril et al., 2011; Hopkins et al., 2017), but based on the record available to us, over 270 million years of evolution, trilobites were characterized by a single pair of antennae followed by series of mostly homogenous biramous pairs of walking legs with respiratory structures and no modification of appendages into specialized mouthparts.

Analysis of character matrix

The unusual nature of the character design limits the types of analyses or comparisons that may be made using this data. For example, a genus with a large proportion of “1” scores may be considered to express a large number of unusual traits. Because not all congeneric species may express that trait, we can also consider this to be a tentative assessment of how disparate species might be within the genus, although this interpretation must be made with caution since it is not readily apparent if a score of “1” indicates that all or only some of the species express that trait. What is more important for our study is the average proportion of “1”s within orders, which summarizes the extent to which genera have species that deviate from the typical trilobite body plan. We calculated the proportion of “1”s within each genus as the number of “1”s divided by the number of characters that could be coded as either “0” or “1”; values range from 0 to 1. Because genera with the same proportion of “1”s may express different combination of traits, we compared the average

proportion of “1”s within orders to the average pairwise distance among genera within orders. The latter summarizes the extent to which genera within orders deviate consistently with other genera. For example, two genera may have both the same number and same combination of “1”s, in which case their pairwise distance would be low, or the same number but different combination of “1”s, in which case their pairwise distance would be high. Pairwise distance was calculated using the arcsine square root of Gower’s distance as implemented in the Claddis package for R (Lloyd, 2016); values range from 0 (no dissimilarity) to 1 (maximal dissimilarity). The arcsine square root transformation is applied because it can be helpful for making proportional data more normally distributed and is the default for Gower’s distance in Claddis (Lloyd 2016). For this dataset, applying the transformation did not change the results. Although some characters have logical dependency, they are not designed within a hierarchical framework and so distance metrics that have been developed to handle hierarchical characters (e.g., Hopkins and St John, 2018) are not necessary.

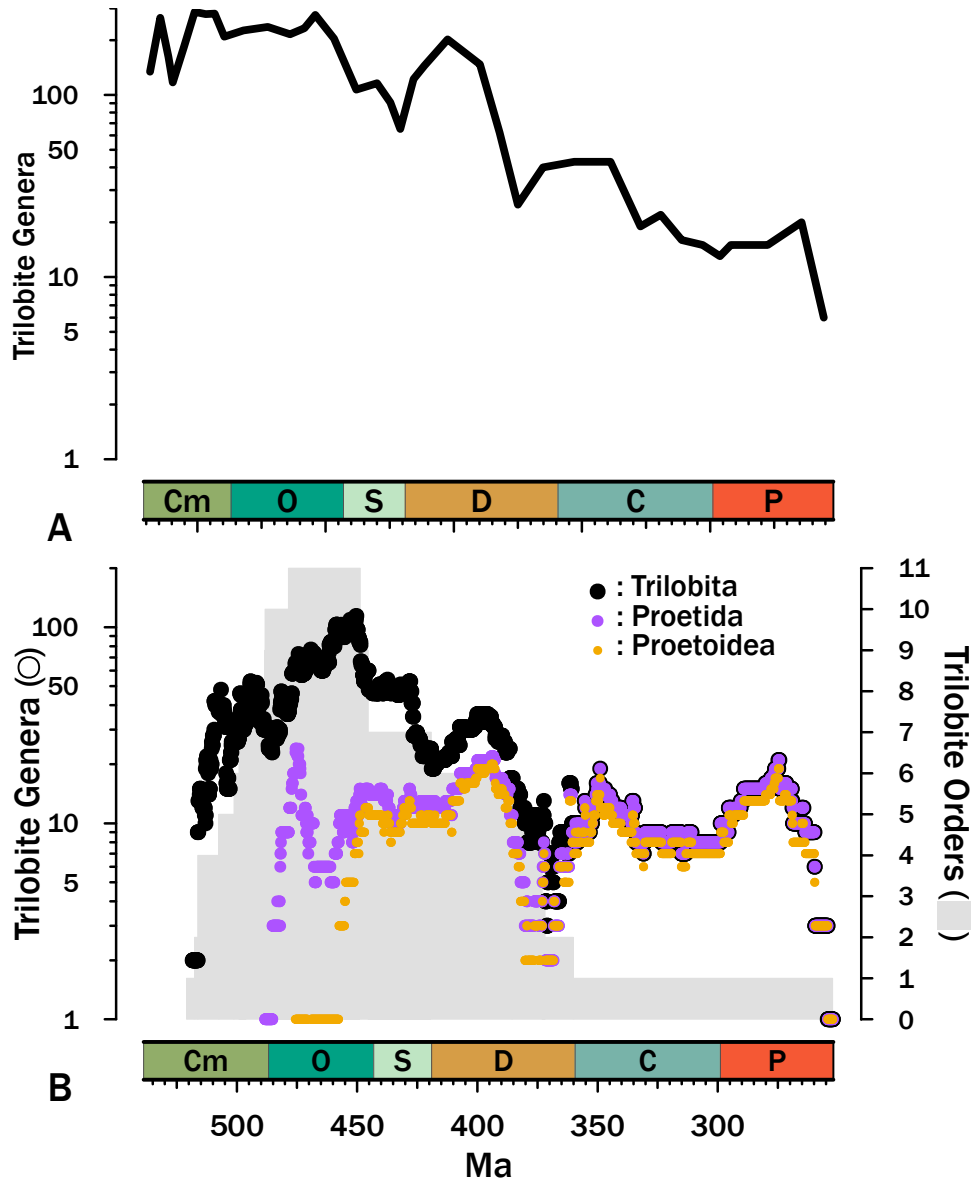
We also produced maps which show the presence of character combinations in each geologic period (Supplementary Figure 4). For all character combinations expressed by Permian trilobites, we determined the earliest geologic period in which that character combination was expressed. The lower right off-diagonal gives the character state combinations possessed by Permian proetides. (Because state-pair matrices are symmetrical, all relevant information is in the off-diagonal of each matrix.) The upper left off-diagonal gives the combinations possessed by older (Cambrian through Carboniferous) trilobites.

Although we focus on Permian proetides, the Devonian represents the last stand for two other order, the Phacopida and Lichida, which both were quite diverse during the Devonian. We therefore repeated the comparison using only Devonian members of the Proetida, Phacopida and Lichida in order to examine how “living fossil-ish” each order was by then (Supplementary Figure 5). Only the Lichida display any new character state combinations during the Devonian. Like the Permian proetides, Devonian proetides possess no state pairs that first appear after the Silurian. The Devonian Phacopida are even more extreme, as they possess no state pairs that first appear after the Ordovician. However, all three orders including the Lichida possess largely character state combinations that first appear in the Cambrian.

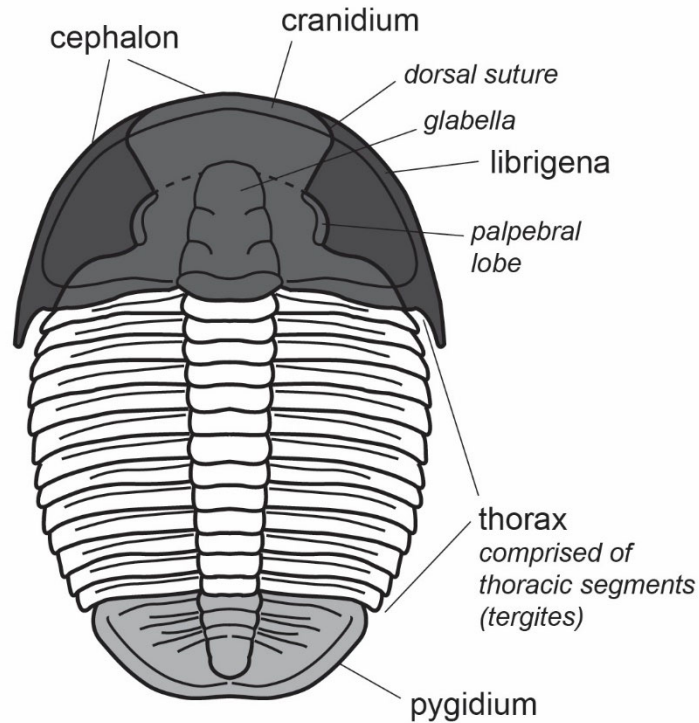
2 Supplementary Figures and Tables

Supplementary Table 1. Results of np-MANOVA. *d* = distance; UCL = upper 95% confidence limit. Z-scores and p-values are based on 1000 random permutations using a residual randomization in permutation procedures (RRPP) (Collyer and Adams, 2018).

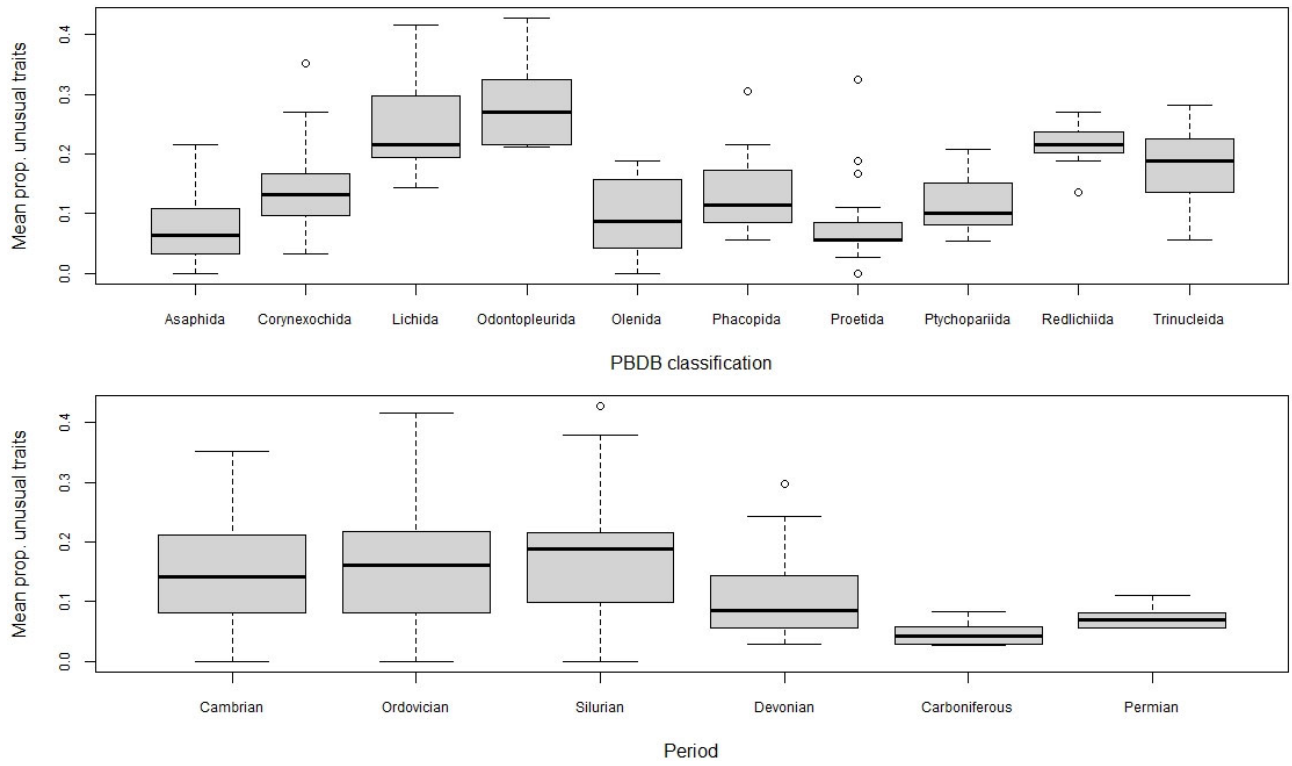
FOOTE DATASET, FULL					E&S DATASET, FULL				
<i>Time:time</i>	<i>d</i>	<i>UCL</i>	<i>Z-value</i>	<i>p-value</i>	<i>Time:time</i>	<i>d</i>	<i>UCL</i>	<i>Z-value</i>	<i>p-value</i>
LC:MC	0.0711	0.0776	1.4083	0.083	LC:MC	0.1082	0.1105	1.5303	0.06
MC:UC	0.0276	0.0492	0.0339	0.487	MC:UC	0.0848	0.0821	1.7756	0.039
UC:EO	0.0340	0.0444	0.8684	0.199	UC:LO	0.1549	0.0715	3.4567	0.001
EO:LO	0.1376	0.0458	5.3056	0.001	LO:MO	0.0579	0.0735	1.1330	0.135
LO:SI	0.0965	0.0496	3.5857	0.001	MO:UO	0.0297	0.0693	-0.1758	0.575
SI:D1	0.0802	0.0919	1.2588	0.11	OU:Sil	0.0547	0.0859	0.6007	0.283
D1:D2	0.0745	0.1022	0.7920	0.223	Sil:LD	0.0488	0.0998	0.0939	0.471
D2:C1	0.1555	0.1068	2.7609	0.002	LD:MD	0.0858	0.0872	1.6181	0.057
C1:C2	0.0462	0.1755	-1.4925	0.933	MD:Ca	0.1302	0.0866	2.5916	0.003
C2:PR	0.0745	0.1832	-0.5331	0.707	Ca:LP	0.0569	0.1317	-0.1422	0.55
					LP:MP	0.0543	0.1533	-0.5079	0.686
					MP:UP	0.0746	0.1512	0.1410	0.45
FOOTE DATASET, PROETIDAE					E&S DATASET, PROETIDAE				
<i>Time:time</i>	<i>d</i>	<i>UCL</i>	<i>Z-value</i>	<i>p-value</i>	<i>Time:time</i>	<i>d</i>	<i>UCL</i>	<i>Z-value</i>	<i>p-value</i>
SI:D1	0.0650	0.1159	0.0881	0.475	UO:MD	0.0906	0.1848	0.1050	0.471
D1:D2	0.0776	0.1007	0.9841	0.164	MD:Ca	0.1014	0.1261	1.1506	0.121
D2:C1	0.0566	0.0688	1.1257	0.141	Ca:LP	0.0466	0.0834	0.4030	0.353
C1:C2	0.0309	0.0876	-1.1299	0.868	LP:MP	0.0418	0.0958	-0.0339	0.51
C2:PR	0.0698	0.0928	0.8095	0.224	MP:UP	0.0629	0.0927	0.8322	0.21
SI:PR	0.0394	0.0978	-0.6948	0.739	UO:UP	0.1211	0.1611	0.9938	0.178



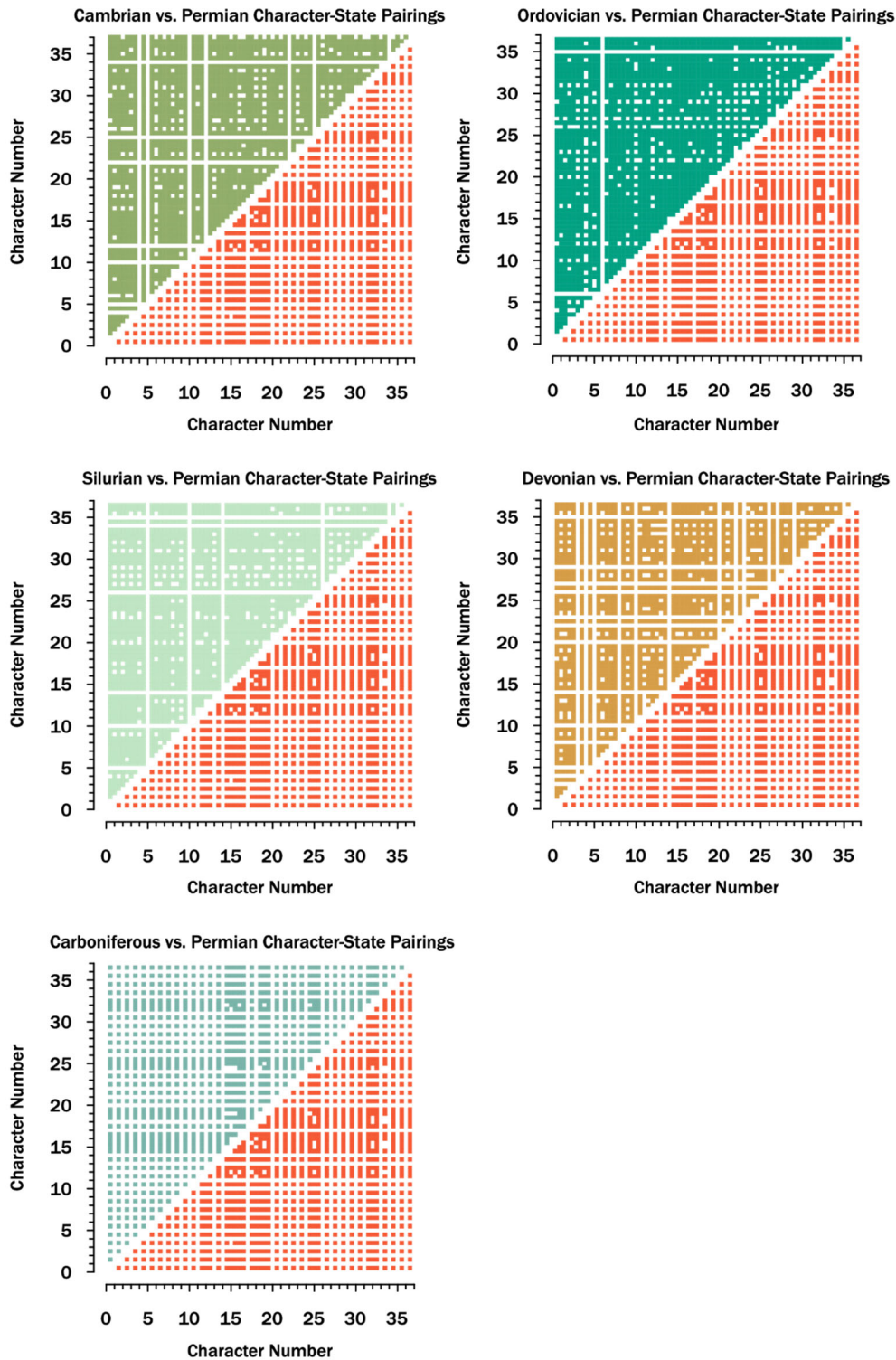
Supplementary Figure 1. Two different depictions of trilobite generic diversity over the Paleozoic. **A.** Within-stage generic diversity of trilobites based on Sepkoski dataset (Sepkoski, 2002) and compiled on 12 Jan 2023 from the Sepkoski’s Online Genus Database constructed and maintained by Shanan Peters (<http://strata.geology.wisc.edu/jack/>). No changes were made to any taxonomic names or first and last appearances. The timescale was updated to that of Gradstein et al. (2020). **B.** Stage-slice boundary-crosser richness (see Foote 2000) given data from the Paleobiology Database downloaded on 12 Feb 2023. Cambrian-Silurian stage-slices are based on Bergström et al. (2009), Cramer et al. (2011) and Rasmussen et al. (2019). Post-Silurian stage-slices as well as updated chronostratigraphic assignments for formations and members in PBDB collections are from Wagner (2020-2021) and subsequent updates (see Congreve et al., 2021). Gray histograms provide the numbers of orders present in each stage-slice. See Supplementary Dataset 3 for supporting RData files and R scripts.



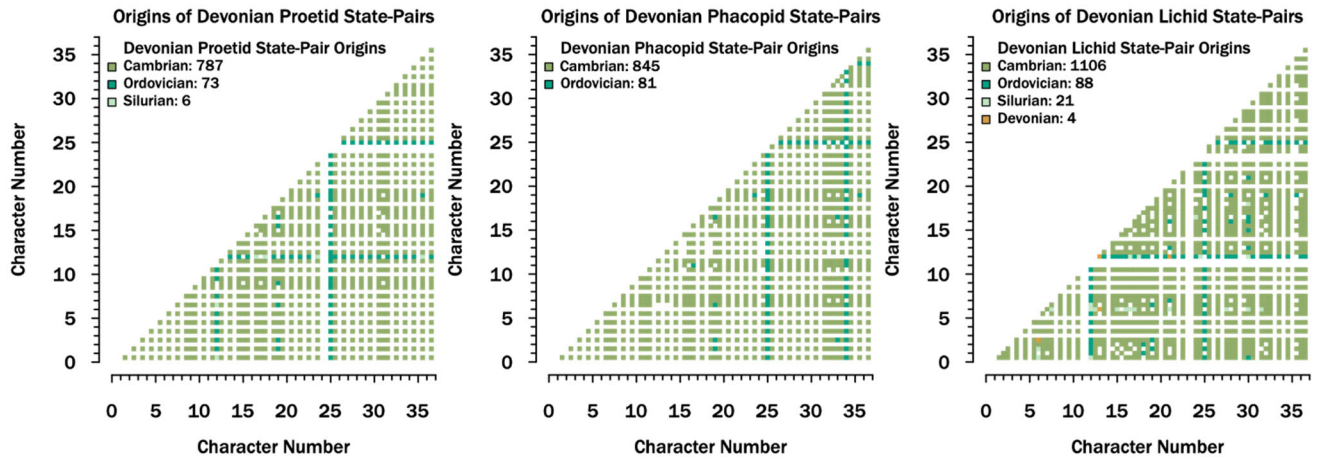
Supplementary Figure 2. Schematic showing the major body regions of the biomineralized exoskeleton, based on *Elrathia kingii* (Meek 1870). The cephalon, or head shield, is comprised of a variable number and type of articulated sclerites. In the vast majority of trilobites, a dorsal suture divided the cephalon into the cranidium and the librigena; additional sutures separated the dorsal sclerites from any ventral sclerites. The post-cephalic region is the trunk, which was comprised of the thorax and the pygidium (tail shield). The thorax itself was comprised of some number (here 13) of articulating sclerites, traditionally referred to as thoracic segments, but arguably better described as tergites in comparison to other arthropods. Modified from Hopkins (2017).



Supplementary Figure 3. Boxplots showing the proportion of unusual traits within orders (upper panel) and within geologic periods (lower panel).



Supplementary Figure 4. Character state-pairs possessed by the coded Permian proetides (lower right) contrasted with character state-pairs possessed by the coded representatives of the Cambrian through Carboniferous (upper left).



Supplementary Figure 5. Character state-pairs possessed by the coded Devonian members of the Proetida, Phacopida and Lichida. Colors reflects when state-pairs first appeared among all trilobites. Only Devonian lichides display “new” character state combinations. However, the preponderance of character state combinations are first sampled among Cambrian trilobites for all three orders.

3. Description of supplementary datasets

Supplementary Dataset 1. Datasets and R scripts for morphometric analysis.

Supplementary Dataset 2. List of the most common trilobite genera within each order within each geologic time period based on occurrences in the Paleobiology Database. See Supplementary Material for description of sampling protocol and for information about the trilobite taxonomic scheme used. See Supplementary Dataset 3 for scripts and other supporting files for generating this list.

Supplementary Dataset 3. RData files and Rscripts in support of diversity through time plots (Supplementary Figure 1), taxon sampling (Supplementary Dataset 2), and analysis of character matrix (Supplementary Dataset 4).

Supplementary Dataset 4. Character descriptions and codings for all sampled genera as well as information about the observed species and litera consulted for coding purposes.

Supplementary Datasets 1, 2, and 3 are archived at AMNH Digital Repository [<https://doi.org/10.5531/sd.paleo.10>].

Supplementary Dataset 4 is archived at morphobank.org, Project 4204 [<https://morphobank.org/permalink/?P4204>].

4. References for Supplementary Material

- Adrain, J.M. (2011). "Class Trilobita Walch, 1771," in *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness*, ed. Z.-Q. Zhang. *Zootaxa* 3148), 104-109.
- Adrain, J.M., McAdams, N.E.B., and Karim, T.S. (2012). The Middle Ordovician bathyurid trilobite *Pseudoolenoides*, with a revised trilobite biostratigraphy of the Dapingian and lower Darriwilian of western Laurentia. *Zootaxa* 3467(1), 1-97.
- Beech, J.D., and Lamsdell, J.C. (2021). Phylogeny, disparity and mass extinction response in the trilobite order Harpetida. *Papers in Palaeontology* 7(4), 2205-2225. doi: <https://doi.org/10.1002/spp2.1399>.
- Benton, M.J., Ruta, M., Dunhill, A.M., and Sakamoto, M. (2013). The first half of tetrapod evolution, sampling proxies, and fossil record quality. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372, 18–41. doi: 10.1016/j.palaeo.2012.09.005.
- Bergström, S.M., Chen, X., Gutierrez-Marco, J.C., and Dronov, A. (2009). The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia* 42(1), 97-107. doi: <https://doi.org/10.1111/j.1502-3931.2008.00136.x>.
- Bignon, A., Waisfeld, B.G., Vaccari, N.E., and Chatterton, B.D.E. (2020). Reassessment of the Order Trinucleida (Trilobita). *Journal of Systematic Palaeontology* 18(13), 1061-1077. doi: 10.1080/14772019.2020.1720324.
- Billings, E. (1861). *New species of Lower Silurian fossils. 1. On some new or little-known species of Lower Silurian fossils from the Potsdam Group (Primordial Zone)*. Montreal: Geological Survey of Canada.
- Brown, J.H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist* 124(2), 255–279. doi: 10.2307/2461494.
- Choi, D.K., Kim, E.-Y., and Lee, J.G. (2008). Upper Cambrian polymerid trilobites from the Machari Formation, Yongwol, Korea. *Geobios* 41(2), 183-204. doi: <http://dx.doi.org/10.1016/j.geobios.2007.05.005>.
- Collyer, M.L., and Adams, D.C. (2018). RRPP: An R package for fitting linear models to high-dimensional data using residual randomization. *Methods in Ecology and Evolution* 9(7), 1772-1779.
- Collyer, M.L., Sekora, D.J., and Adams, D.C. (2014). A method for analysis of phenotypic change for phenotypes described by high-dimensional data. *Heredity*. doi: 10.1038/hdy.2014.75.
- Congreve, C.R., Patzkowsky, M.E., and Wagner, P.J. (2021). An early burst in brachiopod evolution corresponding with significant climatic shifts during the Great Ordovician Biodiversification Event. *Proceedings of the Royal Society B* 288(1958), 20211450.

- Cramer, B.D., Brett, C.E., Melchin, M.J., Männik, P., Kleffner, M.A., McLaughlin, P.I., et al. (2011). Revised correlation of Silurian Provincial Series of North America with global and regional chronostratigraphic units and $\delta^{13}\text{C}_{\text{carb}}$ chemostratigraphy. *Lethaia* 44(2), 185-202.
- Dunhill, A.M., Benton, M.J., Twitchett, R.J., and Newell, A.J. (2012). Completeness of the fossil record and the validity of sampling proxies at outcrop level. *Palaeontology* 55(6), 1155–1175. doi: 10.1111/j.1475-4983.2012.01149.x.
- Foote, M. (1989). Perimeter-based Fourier analysis: a new morphometric method applied to the trilobite cranidium. *Journal of Paleontology* 63(6), 880-885.
- Foote, M. (1991). Morphologic patterns of diversification: examples from trilobites. *Palaeontology* 34(2), 461-485.
- Foote, M. (1993). Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* 19(2), 185-204. doi: 10.1017/S0094837300015864.
- Foote, M. (2000). Origination and extinction components of taxonomic diversity: general problems. *Paleobiology*, 74-102.
- Foote, M., and Raup, D.M. (1996). Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* 22(2), 121 – 140. doi: 10.1666/0094-8373-22.2.121.
- Fortey, R.A. (1997). "Classification," in *Treatise of Invertebrate Paleontology. Pt. O. Trilobita (Revised)*. ed. R.L. Kaesler. Geological Society of America and University of Kansas Press, Lawrence), 289-302.
- Fortey, R.A., and Owens, R.M. (1975). Proetida--a new order of trilobites. *Fossils and Strata* 4, 227-239.
- Fortey, R.A., and Owens, R.M. (1991). A trilobite fauna from the highest Shineton Shales in Shropshire, and the correlation of the latest Tremadoc. *Geological Magazine* 128(5), 437-464.
- Gradstein, F.M., Ogg, J.G., Schmitz, M.D., and Ogg, G.M. (2020). *Geologic time scale 2020*. Elsevier.
- Guillerme, T., Cooper, N., Brusatte, S.L., Davis, K.E., Jackson, A.L., Gerber, S., et al. (2020). Disparities in the analysis of morphological disparity. *Biology Letters* 16(7), 20200199. doi: doi:10.1098/rsbl.2020.0199.
- Harrington, H.J. (1956). Olenellidae with advanced cephalic spines. *Journal of Paleontology* 30(1), 56-61.
- Harrington, H.J., Henningsmoen, G., Howell, B.F., Jaanusson, V., Lochman-Balk, C., Moore, R.C., et al. (1959). *Treatise of Invertebrate Paleontology. Pt O. Arthropoda 1, Trilobita*. Geological Society of America and University of Kansas Lawrence Press, Lawrence.
- Hawle, I., and Corda, A.J.C. (1847). Prodröm einer Monographie der böhmischen Trilobiten. *Königliche Böhmisches Gesellschaft der Wissenschaften, Abhandlungen* 5, 1-176.
- 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(4), 295-334.

- Hopkins, M.J. (2011). Species-level phylogenetic analysis of some pterocephaliids (Trilobita) from the Great Basin, western USA. *Journal of Paleontology* 85, 1128-1153.
- Hopkins, M.J. (2014). The environmental structure of trilobite morphological disparity. *Paleobiology* 40(3), 352-373. doi: 10.1666/13049.
- Hopkins, M.J. (2017). Development, trait evolution, and the evolution of development in trilobites. *Integrative and Comparative Biology* 57(3), 488-498. doi: 10.1093/icb/icx033.
- Hopkins, M.J., Chen, F., Hu, S., and Zhang, Z. (2017). The oldest known digestive system consisting of both paired digestive glands and a crop from exceptionally preserved trilobites of the Guanshan Biota (Early Cambrian, China). *PLOS ONE* 12(9), e0184982. doi: 10.1371/journal.pone.0184982.
- Hopkins, M.J., and Gerber, S. (2017). "Morphological Disparity," in *Evolutionary Developmental Biology: A Reference Guide*, eds. L. Nuno de la Rosa & G. Müller. (Cham: Springer International Publishing), 1-12.
- Hopkins, M.,J., and St John, K. (2018). A new family of dissimilarity metrics for discrete character matrices that include inapplicable characters and its importance for disparity studies. *Proceedings of the Royal Society B: Biological Sciences* 285(1892), 20181784. doi: 10.1098/rspb.2018.1784.
- Hou, J.-b., Hughes, N.C., and Hopkins, M.J. (2021). The trilobite upper limb branch is a well-developed gill. *Science Advances* 7(14), eabe7377. doi: doi:10.1126/sciadv.abe7377.
- Hou, J.-b., Hughes, N.C., and Hopkins, M.J. (2023). Gill grooming in middle Cambrian and Late Ordovician trilobites. *Geological Magazine*. Doi: 10.1017/S001675682300002X.
- Hughes, N.C. (2003). Trilobite tagmosis and body patterning from morphological and developmental perspectives. *Integrative and Comparative Biology* 43, 185-206.
- Hurlbert, A.H., and White, E.P. (2007). Ecological correlates of geographical range occupancy in North American birds. *Global Ecology and Biogeography* 16(6), 764–773. doi: 10.1111/j.1466-8238.2007.00335.x.
- Jell, P.A., and Adrain, J.M. (2002). Available generic names for trilobites. *Mem. Queensl. Mus.* 48, 331-553.
- Kobayashi, T. (1935). The Cambro-Ordovician formations and faunas of South Chosen. Paleontology. Part 3: Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. *Journal of the Faculty of Science, Imperial University of Tokyo (Section II)* 4, 49-344.
- Lamsdell, J.C., and Selden, P.A. (2015). Phylogenetic support for the monophyly of proetide trilobites. *Lethaia* 48(3), 375-386.
- Lerosey-Aubril, R., Hegna, T.A., and Olive, S. (2011). Inferring internal anatomy from the trilobite exoskeleton: the relationship between frontal auxiliary impressions and the digestive system. *Lethaia* 44(2), 166-184. doi: 10.1111/j.1502-3931.2010.00233.x.
- Lieberman, B.S. (1999). Systematic revision of the Olenelloidea (Trilobita, Cambrian). *Bulletin of the Peabody Museum of Natural History* 45.

- Liow, L.H. (2013). Simultaneous estimation of occupancy and detection probabilities: an illustration using Cincinnati brachiopods. *Paleobiology* 39(2), 193–213. doi: 10.1666/12009.
- Lloyd, G.T. (2016). Estimating morphological diversity and tempo with discrete character-taxon matrices: implementation, challenges, progress, and future directions. *Biological Journal of the Linnean Society* 118(1), 131-151. doi: 10.1111/bij.12746.
- Losso, S.R., and Ortega-Hernández, J. (2022). Claspers in the mid-Cambrian *Olenoides serratus* indicate horseshoe crab-like mating in trilobites. *Geology* 50(8), 897-901.
- Lu, Y. (1964). "Trilobites," in *Index Fossils of South China*, ed. Y. Wang. (Beijing), 31-41.
- Lu, Y., and Lin, H. (1980). The boundary of Cambrian-Ordovician in western Zheliang and the trilobites contained in it. *Acta Palaeontologica Sinica* 19(2), 59-76.
- Meek, F.B. (1870). Descriptions of fossils collected by U.S. Geological Survey. *Proceedings of the Academy of the Natural Sciences of Philadelphia* (56-64).
- Owen, A.W., and Bruton, D.L. (1980). Late Caradoc-early Ashgill trilobites of the central Oslo Region, Norway. *Paleontological Contributions from the University of Oslo* 245.
- Palmer, A.R., and Repina, L.N. (1993). Through a glass darkly: taxonomy, phylogeny, and biostratigraphy of the Olenellina. *University of Kansas Paleontological Contributions* 3, 1-35.
- Pérez-Peris, F., Laibl, L., Vidal, M., and Daley, A.C. (2021). Systematics, morphology, and appendages of an Early Ordovician pilekiine trilobite *Anacheirurus* from Fezouata Shale and the early diversification of Cheiruridae. *Acta Palaeontologica Polonica* 66(4), 857-877.
- Plotnick, R.E., and Wagner, P. (2018). The greatest hits of all time: the histories of dominant genera in the fossil record. *Paleobiology* 44(3), 368-384. doi: 10.1017/pab.2018.15.
- Příbyl, A. (1949). On several new or little known trilobites of the Devonian of Bohemia [O několika nových nebo málo známých trilobitech z českého devonu]. *Věstník Státní geologický ústav Czechoslovakia* 24, 293-311.
- Ramsköld, L., and Edgecombe, G.D. (1996). Trilobite appendage structure--Eoredlichia reconsidered. *Alcheringa: An Australasian Journal of Palaeontology* 20, 269-276.
- Rasmussen, C.M.Ø., Kröger, B., Nielsen, M.L., and Colmenar, J. (2019). Cascading trend of Early Paleozoic marine radiations paused by Late Ordovician extinctions. *Proceedings of the National Academy of Sciences* 116(15), 7207-7213. doi: 10.1073/pnas.1821123116.
- Raup, D.M., and Boyajian, G.E. (1988). Patterns of generic extinction in the fossil record. *Paleobiology* 14(2), 109 – 125.
- Reed, F.R.C. (1931). XLIII.—A review of the British species of the Asaphidae. *Annals and Magazine of Natural History* 7(41), 441-472. doi: 10.1080/00222933108673332.
- Richter, R. (1932). "Crustacea (Palaeontologie)," in *Handwörterbuch der Naturwissenschaften*, eds. R. Dittler, G. Joos, E. Korschelt, G. Linek, F. Oltmanns & K. Schaum. (Jena: Gustav Fisher), 840-864.

- Rosova, A.V. (1963). Biostratigraphic scheme of the Upper and Upper-Middle Cambrian and new Upper Cambrian trilobites. *Geologiya i Geofizika* 9, 3-20.
- Salter, J.W. (1864). *A monograph of British trilobites from the Cambrian, Silurian, and Devonian formations*. London: Printed for The Palæontographical Society.
- Sepkoski, J.J. (2002). A compendium of fossil marine animal genera. *Bulletins of American paleontology* 363, 1-560.
- Siveter, D.J., Fortey, R.A., Briggs, D.E., Siveter, D.J., and Sutton, M.D. (2021). The first Silurian trilobite with three-dimensionally preserved soft parts reveals novel appendage morphology. *Papers in Palaeontology* 7(4), 2245-2253.
- Steininger, J. (1831). Observations sur les fossiles du calcaire intermediaire de L'Eifel. *Mémoires de la Société géologique de France* 1(15), 331-371.
- Suárez, M.G., and Esteve, J. (2021). Morphological diversity and disparity in trilobite cephalae and the evolution of trilobite enrolment throughout the Palaeozoic. *Lethaia* 54(5), 752-761. doi: 10.1111/let.12437.
- Swinnerton, H.H. (1915). Suggestions for a revised classification of trilobites. *Geological Magazine* 6(2), 487-496, 538-545.
- Ulrich, E.O. (1924). Notes on new names in the table of formations and on physical evidence of breaks between the Paleozoic systems in Wisconsin. *Transactions of the Wisconsin Academy of Sciences* 21, 71-107.
- Wagner, P.J. (2020 - 2021). "Rock_Unit Database.RData". (https://github.com/PeterJWagner3/PaleoDB_for_RevBayes_Webinar/tree/master/R_Projects/Data_for_R).
- Wagner, P.J., Plotnick, R.E., and Lyons, S.K. (2018). Evidence for trait-based dominance in occupancy among fossil taxa and the decoupling of macroecological and macroevolutionary success. *The American Naturalist* 192(3), E120 – E138. doi: 10.1086/697642.
- Walcott, C.D. (1885). New genus of Cambrian trilobites, *Mesonacis*. *American Journal of Science* 3(29), 328-330.
- Walcott, C.D. (1910). *Olenellus and Other Genera of the Mesonacidae*. Smithsonian Institution.
- Wallerius, F. (1895). *Undersök ningar öfver zonen med agnostus laevigatus in Vestergötland*. Lund.
- Whiteley, T.E., Kloc, G.J., and Brett, C.E. (2002). *Trilobites of New York: an illustrated guide*. Ithaca, NY: Cornell University Press.
- Whittington, H.B. (2002). Lichidae (Trilobita): morphology and classification. *Journal of Paleontology* 76(2), 306-320.
- Whittington, H.B. (2009). The Corynexochina (Trilobita): a poorly understood suborder. *Journal of Paleontology* 83(1), 1-8.
- Whittington, H.B., Chatterton, B.D.E., Speyer, S.E., Fortey, R.A., Owens, R.M., Chang, W.T., et al. (1997). "Trilobita (revised edition)," in *Treatise on Invertebrate Paleontology, Pt. O*,

Arthropoda 1, ed. R.C. Moore. (Lawrence: Geological Society of America and The University of Kansas Press), 1 - 530.

Wilson, J.L. (1956). Revisions in Nomenclature and New Species of Cambro-Ordovician Trilobites from the Marathon Uplift, West Texas. *Journal of Paleontology* 30(6), 1341-1349.

Yuan, J.-L., and Yin, G.-Z. (1998). New polymerid trilobites from the Chefu Formation in Early Late Cambrian of eastern Guizhou. *Acta Palaeontologica Sinica* 37(2), 138-172.