



**CATEGORICAL VERSUS GEOMETRIC MORPHOMETRIC  
APPROACHES TO CHARACTERISING THE EVOLUTION OF  
MORPHOLOGICAL DISPARITY IN OSTEOSTRACI  
(VERTEBRATA, STEM-GNATHOSTOMATA)**

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Complete List of Authors:	Ferrón, Humberto; Universitat de Valencia Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Greenwood, Jenny; University of Bristol School of Earth Sciences Deline, Bradley; University of West Georgia, Geosciences Martínez Pérez, Carlos; Universitat de Valencia Institut Cavanilles de Biodiversitat i Biologia Evolutiva, ; University of Bristol School of Biological Sciences, BOTELLA, HECTOR; university of Valencia, geology Sansom, Robert; University of Manchester, School of Earth and Environmental Sciences Ruta, Marcello; University of Lincoln, Life Sciences; Donoghue, Philip; University of Bristo, School of Earth Sciences
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3 **CATEGORICAL VERSUS GEOMETRIC MORPHOMETRIC APPROACHES TO CHARACTERISING THE EVOLUTION**  
4 **OF MORPHOLOGICAL DISPARITY IN OSTEOSTRACI (VERTEBRATA, STEM-GNATHOSTOMATA)**  
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8 *by* HUMBERTO G. FERRÓN<sup>1,2\*</sup>, JENNY M. GREENWOOD<sup>1</sup>, BRADLEY DELINE<sup>3</sup>, CARLOS MARTÍNEZ-PÉREZ<sup>1,2</sup>,  
9 HÉCTOR BOTELLA<sup>2</sup>, ROBERT S. SANSOM<sup>4</sup>, MARCELLO RUTA<sup>5</sup> *and* PHILIP C. J. DONOGHUE<sup>1\*</sup>  
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12  
13 <sup>1</sup>School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, UK; e-  
14 mail: humberto.ferron@bristol.ac.uk, carlos.martinez-perez@bristol.ac.uk, phil.donoghue@bristol.ac.uk

15  
16 <sup>2</sup>Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, C/ Catedràtic José Beltrán  
17 Martínez, 2, 46980 Paterna, Valencia, Spain; e-mails: humberto.ferron@uv.es, carlos.martinez-perez@uv.es,  
18 hector.botella@uv.es  
19

20  
21 <sup>3</sup>Department of Geosciences, University of West Georgia, Carrollton, GA 30118, USA; e-mail:  
22 bdeline@westga.edu  
23

24  
25 <sup>4</sup>School of Earth & Environmental Sciences, University of Manchester, Manchester, M13 9PT, UK; e-mail:  
26 robert.sansom@manchester.ac.uk  
27

28 <sup>5</sup>School of Life Sciences, University of Lincoln, Riseholme Hall, Lincoln LN2 2LG, UK ; e-mail:  
29 MRuta@lincoln.ac.uk  
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33 \*Corresponding authors  
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36 **ABSTRACT**

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38 Morphological variation (disparity) is almost invariably characterised by two non-mutually exclusive  
39 approaches: (i) quantitatively, through geometric morphometrics, and (ii) in terms of discrete, 'cladistic', or  
40 categorical characters. Uncertainty over the comparability of these approaches diminishes the potential to  
41 obtain nomothetic insights into the evolution of morphological disparity and the few benchmarking studies  
42 conducted so far show contrasting results. Here, we apply both approaches to characterising morphology in  
43 the stem-gnathostome clade Osteostraci in order to assess congruence between these alternative methods  
44 as well as to explore the evolutionary patterns of the group in terms of temporal disparity and the influence  
45 of phylogenetic relationships and habitat on morphospace occupation. Our results suggest that both  
46 approaches yield similar results in morphospace occupation and clustering, but also some differences  
47 indicating that these metrics may capture different aspects of morphology. Phylomorphospaces reveal  
48 convergence towards a generalised 'horseshoe'-shaped cranial morphology and two strong trends involving  
49 major groups of osteostracans (benneviaspidids and thyeistiids), which probably reflect adaptations to  
50 different lifestyles. Temporal patterns of disparity obtained from categorical and morphometric approaches  
51 appear congruent, however disparity maxima are recorded at very different times in the evolutionary history  
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3 of the group when increasing the number of taxa and characters in the categorical dataset. The results of our  
4 analyses indicate that categorical and continuous datasets may characterize different patterns of  
5 morphological disparity and that discrepancies could reflect preservational limitations of morphometric data  
6 and differences in the potential of each data type for characterizing more or less inclusive aspects of overall  
7 phenotype.  
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13 **Key words:** disparity, morphospace, categorical data, geometric morphometrics, Osteostraci  
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16 QUANTIFICATION of morphology and morphological disparity is integral to assessing general macroevolutionary  
17 patterns in the fossil record, such as adaptive radiations, rates of evolution, responses to extinctions, biotic  
18 replacements, and the existence of constraints on form (Foote 1997 and references therein). Consequently,  
19 there have been many attempts to evaluate the impact of potential biasing factors on morphological disparity  
20 estimates, including the possible influence of taphonomy (Webster & Hughes 1999; Bariş 2017), taxonomic  
21 or geographic scale (Butler *et al.* 2012; Deline *et al.* 2012), environmental distribution (Hopkins 2014),  
22 community structure (Deline 2009), sampling all or only a subset of whole-organism characteristics (Foth *et*  
23 *al.* 2012; Hopkins 2017), choice of metric (Ciampaglio *et al.* 2001), character selection (Deline & Ausich 2017),  
24 and choice of methodology (Villier & Eble 2004; Hetherington *et al.* 2015; Hopkins 2017).  
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33 Morphological disparity and morphospace occupation patterns have conventionally been based on two non-  
34 mutually exclusive approaches to characterising morphology. Firstly, through geometric morphometrics,  
35 morphology is characterised quantitatively in terms of continuous variation in aspects of organismal  
36 morphology (e.g., Stayton & Ruta 2006). This approach is most commonly used to assess morphospace  
37 occupation at lower taxonomic levels due to the need for homologous features in all specimens within a  
38 single study (Wills *et al.* 1994; Bookstein 1997). Therefore, while these methods are very sensitive to  
39 morphological variation, their power diminishes with increasing taxonomic scale reflecting the concomitant  
40 reduction in the number of universally shared homologous features (Hetherington *et al.* 2015). Alternatively,  
41 morphology can be characterised in terms of discrete or categorical characters of the sort most commonly  
42 employed in the cladistic analysis of morphology. This approach to characterising morphology is usually  
43 undertaken in analyses of broad taxonomic scope, where there are large numbers of categorical differences  
44 between taxa, but fewer universal homologous structures that might serve as a basis for geometric  
45 morphometrics. As such, the categorical characterization of morphology can capture more unique aspects of  
46 form, including autapomorphic features (Briggs *et al.* 1992; Wills 1998). However, this approach is also much  
47 less sensitive to morphological variation and, as such, it may underestimate disparity. Despite the differences  
48 between these approaches, most of the small number of benchmarking studies that have been conducted  
49 have shown that continuous and categorical approaches to characterising morphology yield broadly  
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3 congruent patterns of disparity (Villier & Eble 2004; Anderson & Friedman 2012; Foth *et al.* 2012;  
4 Hetherington *et al.* 2015; Hopkins 2017). Nevertheless, Mongiardino Koch and colleagues (2017) have shown  
5 that these two approaches yield contrasting patterns of disparity in their analysis of the scorpion genus  
6 *Brachistosternus*. This difference may reflect the difference in power of continuous versus categorical  
7 approaches to characterising morphology at different taxonomic scales. However, this study may also reflect  
8 the fact that benchmarking studies remain small in number and many more such studies are needed from  
9 which to gain nomothetic insights into whether different approaches to characterising morphology impact  
10 on the perception of the ensuing patterns of morphological disparity and the evolutionary processes that are  
11 inferred from them. To that end, we explore the evolution of morphological disparity in osteostracans, the  
12 extinct clade of jawless stem-gnathostomes that is generally perceived to be most closely related to jawed  
13 vertebrates (Donoghue *et al.* 2000; Donoghue & Keating 2014; Sansom 2008, 2009a; Scott & Wilson 2015).  
14 As such, the evolution of morphological disparity within this clade is interesting in its own right, as a parallel  
15 to its sister-lineage of jawed vertebrates. However, cranial shape characters contribute extensively to the  
16 systematics of the group (Sansom 2009a), making osteostracans an ideal basis for benchmarking the  
17 characterization of morphology for disparity analysis in terms of discrete or categorical characters. We  
18 characterise the morphology of this clade based on the distinctive and character-rich headshield, both in  
19 terms of geometric morphometric and discrete categorical 'cladistic' data. We compare perceptions of  
20 morphological disparity based on these data sets and, further, interpret the results in terms of their  
21 implications for understanding this temporal, phylogenetic and ecological context of the evolution of this key  
22 clade.  
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### 38 ***Osteostraci as case study***

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40 Osteostracans constitute a clade of extinct jawless vertebrates that ranges from the Llandovery (lower  
41 Silurian) to the Frasnian (Upper Devonian) (Sansom 2009a). Osteostracans are a taxonomically and  
42 morphologically diverse group, characterized by a semicircular dermal headshield encompassing the cranial  
43 and pectoral regions, a number of cephalic fields, pineal foramen, nasohypophysial opening, and a  
44 postcranial body covered in thick scales. Cornual and/or rostral processes extending from the headshield are  
45 well developed in a number of independent lineages and paired fins are present in many taxa but lost in  
46 others (Janvier 1985) - or they evolved convergently between jawed vertebrates and derived Osteostraci  
47 (Denison 1951). Most osteostracans have headshields that are strongly oblate dorso-ventrally although some  
48 have a more approximately circular or prolate in cross-sectional profile (Janvier 1996) (Fig. 1A and B).  
49 Remarkably, such morphological disparity, despite being a potential source of valuable biological and  
50 ecological information (e.g., Janvier & Lawson 1985; Belles-Isles 1987; Bunker & Machin 1991; Afanassieva  
51 1992; Mark-Kurik 1992; Janvier 1996; Morrissey *et al.* 2004; Davies 2009), has not been analysed  
52 quantitatively.  
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## MATERIALS AND METHODS

### *Geometric morphometric analysis*

Our study was confined principally to species of established genera, although a small number of taxa with resolved phylogenetic affinity have also been included, enabling comparison with the most complete osteostracan phylogeny (Sansom 2009a) (Fig. 1C). The study was conducted at genus level, with each genus represented by a single specimen. The type species and holotype specimen for the genus was used except where this specimen was poorly preserved or unavailable for characterization; in such circumstances another well-defined species was used. A total of 29 specimens were included in the geometric morphometric analysis (Fig. 1C). Some specimens exhibit minor deformation, principally due to dorso-ventral compression. No attempt was made to correct for deformation as this would lead to the inclusion of human error and preliminary studies have suggested that biological signal is still well preserved when deformation is minor (Angielczyk & Sheets 2007). Images of specimens for digitization were obtained from photographs of original specimens (see Appendix S1 and File S1). When complete specimens could be pieced together from counterparts, images of these counterparts were superimposed (see Appendix S1 for a list of sources and information on the nature of deformation of these specimens). A total of 123 landmarks of type I, II and III were digitized on selected images using TpsDig v.2.26 (Rohlf 2016a) (Fig. 1B). The choice of landmarks was (by definition) constrained by homology (Bookstein 1997), but also by preservation. Therefore, only frequently preserved characters were included as landmarks in the study. Landmarks of type III were equally interpolated along the specimen outlines in six separate open curves. The number of landmarks chosen to represent each curve reflects the relative length and complexity of each portion of the headshield and was determined visually. TpsRelw v.1.65 (Rohlf 2016b) was used to fit landmark coordinates of all specimens by generalised Procrustes superimposition to remove variation in rotational, scale and translational differences between specimens so that only geometric information was left.

### *Categorical characters*

Our categorical characterization of osteostracan morphology is based on the cladistic data set of Sansom (2008) which comprises 112 characters and 65 taxa (see Appendix S1). We analysed these data in two ways: (i) the complete dataset including cranial and postcranial characters and (ii) a subset of characters that relate to the cephalothoracic 'headshield', including external shape characters, but also neurocranial and histological features. Analyses of this subset of cranial characters facilitates direct comparisons to the analyses of the geometric morphometric data which are similarly limited to the headshield.

### *Disparity quantification from categorical and morphometric data*

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3 The disparity of osteostracans was explored from temporal, phylogenetic and ecological perspectives  
4 considering stratigraphic ranges, phylogenetic relationships, major taxa and habitat interpretations  
5 established in Sansom (2009a) and Sansom *et al.* (2015). Disparity was quantified from both categorical and  
6 continuous character data sets in two different ways: (1) the preordination distance, which is the average  
7 squared distance between taxa based on the original data and (2) the ratio of generalized variance, which is  
8 the ratio between the taxa within a time bin to the entire dataset (in this case the generalized variance is the  
9 determinant of the covariance matrix from the first three axes of the principal coordinate analysis).

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16 Distance matrices were obtained from both categorical and geometric morphometric data sets (considering  
17 Gower and Euclidean distances, respectively) using the package 'cluster' (Maechler et al. 2019) implemented  
18 in R (R Development Core Team 2017). Distance matrices were then subjected to principal coordinate  
19 analysis in the R package 'ape' (Paradis & Schliep 2018). The same procedure was repeated with a categorical  
20 data subset considering only the 29 genera included in the continuous data analysis. This allowed us to  
21 determine how much of the total morphological disparity was represented by the subset of genera used in  
22 the morphometric analysis and also to assess whether discrete and continuous characterisation of form  
23 yielded similar results. In parallel, Mantel tests were implemented using the R package 'vegan' (Oksanen et  
24 al. 2013) to establish the strength and significance of linear correlations among the distance matrices derived  
25 from each of the data sets.

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35 Morphospaces and phylomorphospaces were constructed using the R packages 'Phytools' (Revell 2012) and  
36 'ggplot2' (Wickham 2016). We followed two alternative approaches to creating phylomorphospaces based  
37 on post- and pre-Ordination Ancestral State Estimation (OASE) (see Lloyd (2018) for a review). In the case of  
38 the pre-ordination procedure, ancestral state reconstruction was achieved through stochastic character state  
39 mapping (Huelsenbeck et al. 2003) using the R packages 'Phytools' (Revell 2012) and 'geomorph' for  
40 categorical and geometric morphometric data respectively. We used the phylogenetic tree from Sansom  
41 (2009) after time-calibration in the R package 'paleotree' (Bapst 2012).

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48 Often comparisons of disparity between groups are more valuable than characterizations of the distribution  
49 of taxa within morphospace. To assess whether the different data types (categorical observations versus  
50 continuous measurements) yield similar conclusions about the relative disparity of groups we randomly  
51 selected 9 taxa and 12 taxa (with no overlap) and calculated the ratio of disparity considering both the  
52 categorical and geometric morphometric data. We selected groups of this size to mirror the largest clades  
53 within the dataset (Benneviaspida and Thyestida). This subsampling routine was repeated 10,000 times. If  
54 both data sets capture similar morphological signals, measures of disparity should be the same or similar and  
55 a positive trend is expected and there should be agreement on the more disparate subsample. Our null model

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3 was based on a simulation approach, involving morphological data evolving under Brownian motion on a  
4 phylogeny (following Schaeffer et al. in rev). We first generated 1000 phylogenetic trees using the topology  
5 from Sansom (2009), time-calibrated 500 times using both the equal (Brusatte et al. 2008) and minimum  
6 branch length (Laurin 2004) dating approaches in the R package 'paleotree' (Bapst 2012). For each of these  
7 trees, tip ages were established by randomly sampling ages between each taxon's first and last stratigraphic  
8 ages. We then simulated both categorical and continuous morphology-like data on all of the 1000 dated  
9 phylogenies. We simulated discrete character data sets in the R package 'dispRity' (Guillaume 2018) using the  
10 equal-rates (ER=Mk) model (Paradis & Schliep 2018). For the model parameters, we randomly sampled  
11 distribution shapes of 0.5, 1 or 2 and rates of 5, 10 or 20 (higher rates increased phylogenetic signal). We  
12 simulated geometric shape data, generating 29 'headshield-like' structures defined by 123 landmark  
13 coordinates for each tree in the R package 'Evomorph' (Cabrera and Giri 2016). As inputs, we considered the  
14 consensus shape of the original analysis as the ancestral morphology and the Procrustes residuals from our  
15 original landmark configurations as co-variance data. The resulting categorical and continuous data sets  
16 where then subjected to similar subsampling routines to those described above and the results were  
17 compared with our empirical data. In this case, the disparity ratios were calculated on randomly selected  
18 groups as well as on the benneviaspidids and the thyestids of each simulated data set, which include 9 and  
19 12 taxa, respectively.

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22 Finally, correlation between disparity and taxonomic diversity over time was evaluated in PASW, considering  
23 the different data sets and disparity metrics; taxonomic diversity data were obtained from Sansom *et al.*  
24 (2015). Correlation on first-difference transformed data were also checked in order to eliminate the role of  
25 autocorrelation.

## 26 27 28 **RESULTS**

### 29 30 31 ***Morphospace occupation and phylomorphospaces***

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33 Plots of taxa in the multivariate space generated from the categorical and geometric morphometric data sets  
34 as well as the percentage of total variance summarized by each axis are shown in Figure 2 and Table 1  
35 respectively. Analysis of both the complete and subsampled categorical data sets recovered similar patterns  
36 of taxon clustering within ordination space (note that the mirroring of taxa on PCo1 and PCo2 is an artefact  
37 of the arbitrary direction of ordination). Ordinations of categorical data sets tend to disperse variance  
38 explained across a large number of axes (Lloyd 2016) and, thus, considering just the first three axes may give  
39 an incomplete view of morphological disparity. However, K-means clustering recovered identical grouping of  
40 taxa using the first three (52.7% variance explained) and the first 15 axes (84.6% variance explained) of the  
41 ordination of categorical data. Therefore, even though considering just a subset of the axes can be  
42 problematic, it is unlikely to play a large role in the major structure and clustering of the current data set.

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3 Benneviaspids and thyeistiids, which cover most of the morphospace, occupy different regions showing only  
4 a small overlapping area. A number of zenaspids are also relatively well separated in both ordinations based  
5 on the complete and subsampled categorical data sets. Non-cornuates (e.g., *Hemicyclaspis*), basal cornuates  
6 (e.g., *Cephalaspis*) and some generalised cornuate forms with uncertain phylogenetic affinities (e.g.,  
7 *Pattenaspis*, *Hildenaspis*, *Mimetaspis*, *Zychaspis*) occupy smaller areas that exhibit significant overlap with  
8 those of other groups in the ordination based on the complete categorical data set, but separate better in  
9 the ordination based on the subsampled data set (mostly on PCo3). Concerning habitats, freshwater and  
10 marine genera are restricted to different areas of the morphospace with brackish representatives in  
11 intermediate positions. This is likely due to the existence of a strong association between taxonomic affinity,  
12 morphology, and habitat in benneviaspids and thyeistiids, which are represented mostly by freshwater and  
13 marine forms respectively. Phylomorphospaces obtained following the post- and pre-ordination methods  
14 show similar patterns. In both cases, two strong branching trends are recognised, one within Benneviaspida  
15 (along PCo2) which is characterised by an antero-lateral extension of the cornua and increasing length of the  
16 rostrum (e.g., *Boreaspis*, *Spatulaspis*, *Hoelaspis*), and another within Thyeistiida (along PCo3), characterised  
17 by a reduction and eventual loss of the cornuae (e.g., *Oeselaspis*, *Witaaspis*). The latter is better represented  
18 in the subsampled data set. Reversals are much more common among non-cornuates, basal and generalised  
19 cornuates, and Zenaspida. The ordination based on the continuous character data set exhibits a similar  
20 pattern of taxon clustering to ordinations based on categorical data sets, but there appears to be a greater  
21 overlap when genera are grouped by both major taxa and habitats. The phylomorphospaces obtained from  
22 the continuous data set following pre- and post-ordination methods are again extremely similar, revealing in  
23 both cases that there is a high degree of morphological convergence towards forms with well-developed  
24 caudally positioned cornual processes, most corresponding to freshwater genera of Benneviaspida (e.g.,  
25 *Ectinaspis*), Thyeistiidae (e.g., *Waengsjoeaspis*), Zenaspida (e.g., *Stensiopelta*) and basal and generalised  
26 cornuates (e.g., *Cephalaspis*, *Mimetaspis*) (towards negative values of PCo1). On the other hand, two similar  
27 branching trends to those recorded by categorical data are here recognizable; a first one within Thyeistiidae  
28 which is characterized by the reduction and loss of cornuae within Thyeistiidae, as captured along the PCo1  
29 and 2, and a second one reflecting a notable development of cornual and rostral processes in  
30 Benneviaspida, both captured along the PCo1 and PCo2.

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52 A comparison of the pre-ordination distances (Cat-Gower, GM- Euclidean) for the continuous and categorical  
53 data sets suggests the existence of strong correlation (Mantel State  $r=0.3098$ ,  $p=0.001$ ). These results  
54 contrast with K-means clustering on the two data sets, existing only around 58% agreement on cluster  
55 placement in the three-cluster solution. The three clusters found in the categorical data are composed of two  
56 groups that are environmentally and largely taxonomically consistent along with a more heterogeneous  
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3 group. The morphometric data has one small group that is taxonomically and environmentally consistent and  
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5 two larger mixed groups.  
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### 8 ***Temporal patterns of morphospace occupation and morphological disparity***

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10 Silurian and Devonian osteostracans occupy disparate regions within the morphospace in all three analyses  
11 showing important differences in taxonomic composition and habitats (Fig. 3). Wenlock and Ludlow age  
12 genera are mainly represented by marine thyeistiids and non-cornuates. Pridolian genera comprise brackish  
13 thyeistiids and non-cornuates that occupy intermediate positions between Wenlock-Ludlow and Devonian  
14 taxa. Devonian genera are mostly represented by freshwater representatives of all major osteostracan  
15 groups. The two measures of disparity we employ, preordination distance and generalized variance, seem to  
16 provide different temporal patterns within each data set (Fig. 4). In the complete cladistic data set, maximum  
17 disparity occurs at the beginning of the clade's history, although a second peak is revealed by the  
18 preordination distance metric in the Emsian (Fig. 4A and B). In the geometric morphometric and categorical  
19 subsets, the recorded temporal patterns of disparity appear congruent for each of the metrics, but differ  
20 strongly with those characterised by the complete categorical data set (compare Fig. 4A and B with Fig. 4C  
21 and D). Thus, the preordination distance metric reveals a peak in disparity in the early Devonian (Lochkovian-  
22 Pragian) whereas generalized variance metric suggests comparatively stable values of disparity through the  
23 evolutionary history of the group. A positive correlation exists between taxonomic diversity and disparity,  
24 measured as generalized variance and preordination distance in the categorical subset. These results remain  
25 the same after detrending data for autocorrelation by applying first-difference transformation (Table 2).  
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### 38 ***Categorical versus continuous measurements of morphology in disparity analyses***

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40 Results derived from the subsampling routines, although displaying an important spread of the data, show  
41 positive trends (Fig. 5A). In fact, significant correlation is detected when considering results derived from  
42 both preordination distance ( $R = 0.186$ ) and generalized variance disparity metrics ( $R = 0.065$ ). In almost half  
43 of the sampled cases, the categorical and the geometric morphometric data sets disagree on which sample  
44 is most disparate (i.e., in 45.0% and 44.8% of the cases when considering preordination distance and  
45 generalized variance disparity metrics respectively), which is also the case for the empirical data from  
46 Benneviaspida and Thyeistida (see red dot in Fig. 5A). Positive trends, consistent with those obtained for the  
47 empirical data, are also detected in the simulated data when considering both the disparity ratios between  
48 randomly selected groups (Preordination distance  $R = 0.233$ , 46.8% disagreement; Generalized variance  $R =$   
49  $0.025$ , 21.3% disagreement; Fig. 5B) and between Benneviaspida and Thyeistida (Preordination distance  $R =$   
50  $0.299$ , 33.0% disagreement; Generalized variance  $R = 0.037$ , 43.9% disagreement; Fig. 5B).  
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## **DISCUSSION**

### ***Osteostracan morphological disparity in space and time***

Overall, both categorical and morphometric approaches to characterising morphology yield similar patterns of morphospace occupation and clustering (Fig. 2). Several forms that exhibit a generalised semi-circular headshield outline, such as non-cornuate genera (e.g., *Hemicyclaspis*) or some basal cornuates, appear very close to the mean form in all analyses, which may be considered as the ancestral state for the group given their early branching topology in osteostracan phylogeny (Sansom 2009). This morphology has been related to a benthic mode of life, where the headshield is oriented flat on the substrate and is able to withstand strong currents, while remaining an agile organism (Bunker and Machin 1991). Phylomorphospaces reveal convergence on this headshield morphology within early-branching zenaspidids, the earliest-branching benneviaspidids and thyeistiids, as well as other cornuate taxa, presumably reflecting the optimality or, rather, the general effectiveness of one successful form. This is also reflected in the fact that this area of the morphospace is much more densely occupied than most others. Two evolutionary trends separated in time are clearly recognizable in the phylomorphospaces, involving different major groups of osteostracans occupying disparate habitats (Figs. 2 and 3). The first such trend is characterised by the reduction and loss of the cornual processes in thyeistiids inhabiting marine environments during the Silurian. This has previously been interpreted as an adaptation to burrowing life habits in the more derived groups including tremataspidids and kiaeraspidids (Janvier & Lawson 1985). The second trend is characterized by the development of long cornual and/or rostral processes in freshwater benneviaspidids, during the Devonian. These structures have been the focus of competing functional interpretations in other early vertebrate groups where they have been interpreted as either locomotory adaptations to enhance lift generation or reduce drag (e.g., Mark-Kurik 1992; Botella & Fariña 2008; Novitskaya 2000; Moloshnikov 2001; Fletcher *et al.* 2014), or for predator deterrence (e.g., Janvier 1977), as the housing for sensory organs (e.g., Voichyshyn 2006), as a substrate anchor (e.g., Dineley 1976; Janvier 1985; Wells & Dorr 1985), or an adaptation to specific feeding habits (e.g., Tarlo 1961; Dineley 1994).

We employed both pre- and post-ordination approaches to phylomorphospace construction, the relative merits of which were considered by Lloyd (2018). Post-ordination approaches are readily and therefore commonly applied, but ancestral values are forced to be within the range of sampled tip values and may lead to an underestimation of convergence. In contrast, post-ordination approaches are more complex, requiring prior estimation of the characteristics of the hypothetical ancestors predicted by phylogenetic, but have some advantages including allowing increased sample size, reconstruction of missing data, and avoiding the assumption that estimated ancestors must fall within the range of tip values. However, the prior inclusion of inferred ancestors in pairwise distances and the ensuing ordination can have the effect of inflating clade disparity, perhaps artefactually. Nevertheless, in this instance, our results indicate that both pre- and post-ordination based approaches to estimating phylomorphospace recovered similar overall patterns (Fig. 2).

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3 Conspicuously, large areas of morphospace characterised by both the categorical and continuous character  
4 data sets remain unoccupied which presumably reflects morphological character combinations and shapes  
5 that are hydrodynamically or functionally inefficient, unexplored as a consequence of phylogenetic or  
6 structural constraints, unpreserved or perhaps unrealised because of insufficient evolutionary time.  
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11 Categorical and continuous character data sets convey different patterns of variation in the range of  
12 morphospace occupation, as do the different measures of disparity. Characterization of disparity with  
13 categorical data suggests that the maximum was established early in osteostracan evolution (Fig. 4A and B),  
14 consistent with the derived nature of some Silurian thyeistiids (Figs. 1 and 3). This pattern is more significant  
15 when measuring disparity from preordination distances. However, capturing disparity with geometric  
16 morphometric data suggests that maximal variation was achieved later in osteostracan phylogeny, in the  
17 Pridolian or early Devonian (depending on the metric used). Overall, both data types appear to evidence a  
18 post-Pragian decline in the morphological disparity of the Osteostraci before their Late Devonian extinction.  
19 This pattern could be interpreted literally, congruent with Janvier & Newman's (2005) hypothesis on the  
20 decline of ostracoderm groups, reflecting an increase of ecological restriction during the Middle and Late  
21 Devonian imposed by changes on marginal marine and freshwater environments and/or food resources,  
22 combined with limited dispersal capability (Sansom 2009b). However, flux in the diversity of osteostracans  
23 through this interval has been interpreted to reflect facies shifts in the rock record (Sansom *et al.* 2015).  
24 Indeed, a Pearson Correlation test (Table 2) finds evidence for a significant correlation between diversity (raw  
25 standing diversity or corrected for ghost lineages) and some metrics of morphological disparity based on the  
26 categorical data. Parallel changes in diversity and disparity most likely reflect the environmentally non-  
27 uniform fossil record (Sansom *et al.* 2015) and the adaptation of osteostracans to the environments in which  
28 they lived.  
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### 43 ***Categorical versus continuous measurements of morphology in disparity analyses***

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45 Categorical observations and continuous measurements are non-mutually exclusive approaches to the  
46 characterization of morphology in analyses of the evolution of morphological disparity. In attempting to  
47 derive nomothetic insights in this sense, to address hypotheses such as the universality of maximal initial  
48 disparity (Hughes *et al.* 2012), or the relationship between disparity and diversification (Foote 1993), it is  
49 important that the aspects of morphological variation summarised in disparity analyses are in some sense  
50 equivalent (Hetherington *et al.* 2015). Given the nature and scope of the phenotypic features that these  
51 approaches can characterise, it could be expected that categorical characters, which usually sample from  
52 across the breadth of phenotype, capture different aspects of morphological disparity to geometric  
53 morphometrics, which is usually focussed on a subsample of overall phenotype as a proxy for the whole.  
54 Furthermore, categorical data sets which, as here, are mostly repurposed cladistic data sets, have a tendency  
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3 to eschew invariant, convergent, and autapomorphic characteristics. Continuous character data sets should  
4 not suffer these same ascertainment biases, but capturing morphological variation through continuous  
5 characters has its own limitations. Principally, this is the need to limit landmarks to homologous structures  
6 present in all taxa and, therefore, the challenge of capturing neomorphic structures and losses. Despite this,  
7 the majority of benchmarking studies have found that categorical and continuous characters capture similar  
8 patterns of morphological disparity (Villier & Eble 2004; Anderson & Friedman 2012; Foth *et al.* 2012;  
9 Hetherington *et al.* 2015; Hopkins 2017).

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16 Our results provide some support for this view, suggesting that the patterns of osteostracan morphological  
17 disparity captured by categorical and continuous characters are correlated when cladistic geometric  
18 morphometric data sets capture equivalent taxa and anatomical components (Fig. 5). However, this result is  
19 not surprising since it is possible to express continuous measurements as categorical states (e.g. Thiele 1993)  
20 and, therefore, it is possible to compile categorical data sets that are equivalent to continuous character data  
21 sets, though they have less information content since they objectively and explicitly summarise continuous  
22 variation. The correlation between the empirical and simulated data implies a strong phylogenetic signal  
23 within the morphological data. However, the empirical data exhibit greater disagreement on the relative  
24 disparity within the groups. Despite this apparent equivalence in the results derived from categorical and  
25 geometric morphometric subsets, patterns of disparity recovered by the complete categorical data set  
26 provide a very different perspective on the evolution of morphological diversity within osteostracans both in  
27 terms of the timing of peak disparity within a clade and the relative disparity between subclades. Therefore,  
28 while both data types appear to capture similar patterns of disparity, the nature of morphometric data (highly  
29 dependent on preservation and limited to areas with recognizable homologous structures) could lead in  
30 practice to very partial results and, ultimately, to conclusions more strongly biased by the vagaries of  
31 preservation.

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45 In a very real sense, it does not matter that these two approaches to summarising morphology results in  
46 different perceptions of morphological variation. They provide different perspectives on the same  
47 phenomenon and that, based on the nature of the data, enriches understanding of the evolution of  
48 morphology within species and clades. Further, these alternative approaches may be better suited to  
49 different questions. For example, characterization of disparity in terms of shape variation may be of greater  
50 importance when exploring the constraining role of the aquatic environment in which osteostracans lived.  
51 Meanwhile, categorical characters may be better suited to capturing the overall disparity of osteostracan  
52 phenotype. In this sense, neither approach is necessarily superior.

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3 Further benchmarking studies are essential and analyses that attempt a more precise equivalence between  
4 the composition of categorical and continuous character data sets could be particularly insightful. The  
5 difference in perspective between categorical data sets, which can sample all aspects of phenotype, and  
6 continuous characters which invariably focus on a small proxy of overall morphology, is illuminating in that  
7 it implies that proxy categorical data sets, so often focussed on subsets of anatomy, will also provide a low  
8 dimensional perspective of disparity that may differ from overall phenotypic disparity, access to which is  
9 already limited by the nature of fossilization.

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3 **Figure 1.** (A) Drawings illustrating the general morphology of two distinct well-known osteostracans  
4 (*Cephalaspis* and *Tremataspis*) in dorsal (d), lateral (l) and frontal views (f). Position of the pectoral fins (pf),  
5 dorsal fin (df), caudal fin (cf) and the headshield (hs) is indicated. (B) Descriptive diagrams showing the  
6 terminology of commonly referred anatomical characters of osteostracan headshield (upper diagram) and  
7 the landmark configuration used in the geometric morphometric analysis (lower diagram). Landmark 1,  
8 anterior tip of the headshield or the rostral process (ant. tip.); Landmark 2, posterior tip of the headshield  
9 (post. tip.); Landmarks 3 and 4, most anterior and most posterior medial points of the nasohypophysial  
10 opening (nas. op.) respectively; Landmark 5, pineal foramen (pi. f.); Landmarks 6 and 7, most anterior and  
11 most posterior medial points of the median field (m. fi.) respectively; Landmarks 8 and 9, most anterior points  
12 of the lateral fields (l. fi.); Landmarks 10 and 11, most posterior points of the lateral fields (l. fi.); Landmarks  
13 12 and 13, points of connection between the headshield and the body; Landmarks 14 and 15, most distal  
14 points of the corneal processes (cor. pr.) ; Landmarks 16-23, most anterior, posterior, lateral and medial  
15 points of the eye orbits (ob.); Landmarks 24-73, landmarks situated between Landmarks 1 and 14 and  
16 between Landmarks 1 and 15; Landmarks 74-103, landmarks situated between Landmarks 14 and 12 and  
17 between Landmarks 15 and 13; Landmarks 104-123, landmarks situated between Landmarks 12 and 2 and  
18 between Landmarks 13 and 2. (C) Phylogenetic hypothesis of the Osteostraci (modified from Samson et al.  
19 2015), highlighting in black the species represented in the geometric morphometric analysis.

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33 **Figure 2.** Morphospace occupation and phylomorphospaces of osteostracans grouped by major taxa and  
34 habitats obtained from categorical and geometric morphometric approaches. Morphospaces and  
35 phylomorphospaces are represented by PCo1 (horizontal), PCo2 (upper vertical) and PCo3 (lower vertical)  
36 axes. Osteostracan phylogenetic relationships and headshield drawings modified from Sansom (2009a). *Taxa*:  
37 1, *Hemicyclaspis*; 2, *Boreaspis*; 3, "*Benneviaspis*" *lankesteri*; 4, *Tauraspis*; 5, *Ectinaspis*; 6, *Spatulaspis*; 7,  
38 "*Benneviaspis*" *longicornis*; 8, *Hoelaspis*; 9, *Camptaspis*; 10, *Oeselaspis*; 11, *Yvonaspis*; 12, *Thyestes*; 13,  
39 *Didymaspis*; 14, *Acrotomaspis*; 15, *Norselaspis*; 16, *Witaaspis*; 17, *Procephalaspis*; 18, *Waengsjoeaspis*; 19,  
40 *Illemoraspis*; 20, *Stensiopelta*; 21, *Trewinia*; 22, *Zenaspis*; 23, *Tegaspis*; 24, *Escuminaspis*; 25,  
41 *Spangenhelmaspis*; 26, *Pattenaspis*; 27, *Hildenaspis*; 28, *Cephalaspis*; 29, *Mimetaspis*.

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50 **Figure 3.** Temporal patterns of morphospace occupation of osteostracans grouped by major taxa and habitats  
51 obtained from categorical and geometric morphometric approaches. Morphospaces are only represented by  
52 PCo1 (horizontal) and PCo2 (vertical) axes. Numbers in the morphospaces refer to taxa in Figure 2.

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57 **Figure 4.** A-C. Temporal patterns of morphological disparity obtained from categorical and geometric  
58 morphometric data calculated as the preordination distance (PD) and as the ratio of generalized variance  
59 (GV). Asterisk denote the categorical total data set including both corporal and headshield characters.  
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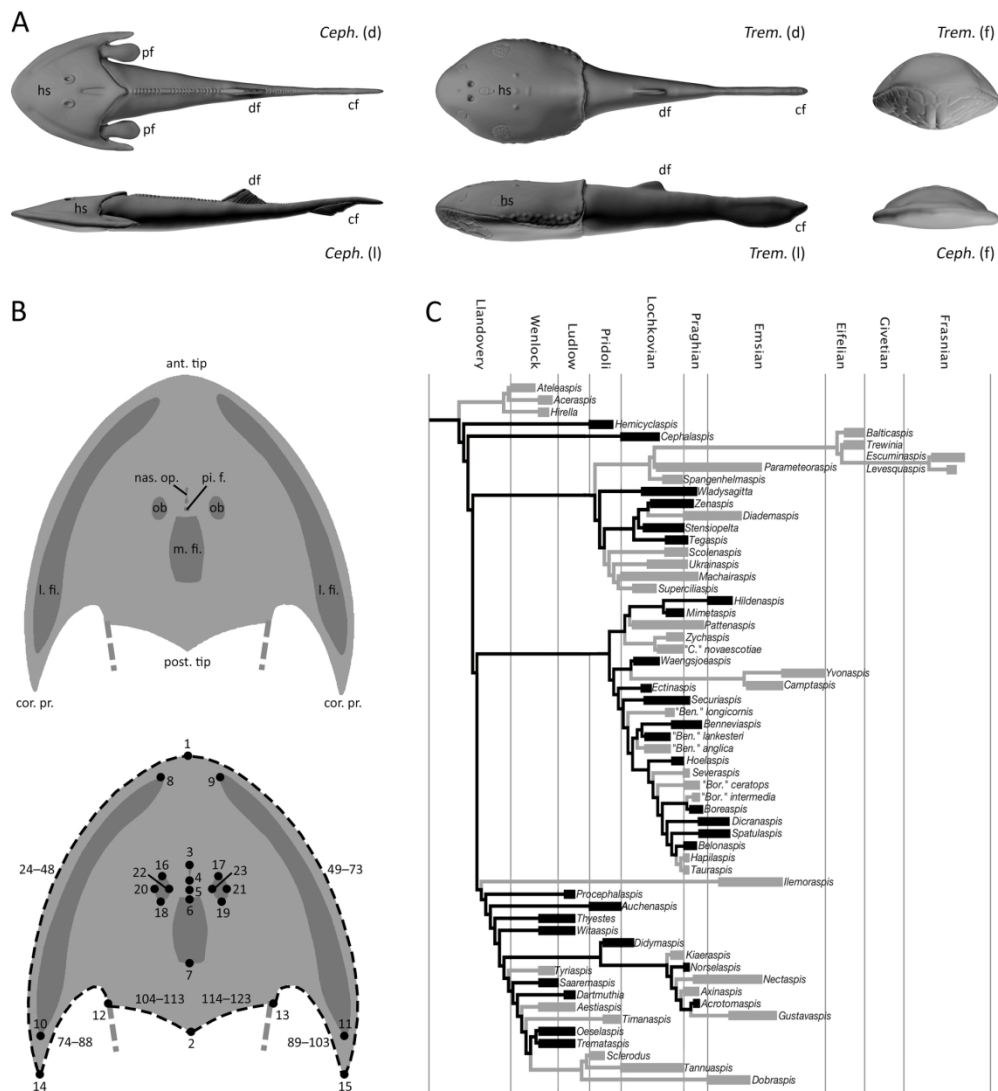
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3 Taxonomic diversity of osteostracans through time based on raw data (RD) and including ghost ranges (GR)  
4 (data taken from Sansom *et al.* 2015). *Timescale*: Ll, Llandovery; We, Wenlock; Lu, Ludlow; Pr, Pridoli; Lo,  
5 Lochkovian; Pg, Pragian; Em, Emsian; M-U Devonian, Middle-Upper Devonian.  
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10 **Figure 5.** Plots showing the disparity ratios derived from the categorical (Csub) and the geometric  
11 morphometric (GM) data sets in both (A) the empirical and (B-C) the modelled approaches. Disparity is  
12 calculated as both the preordination distance (PD) and as the ratio of generalized variance (GV). The disparity  
13 ratios are calculated on two randomly selected groups of 9 and 12 taxa in (A) the empirical and (B) the  
14 modelled data as well as on Benneviaspida and Thyestida in (C) the modelled data. Actual ratio of  
15 Benneviaspida and Thyestida (B/T) is denoted by an asterisk in the empirical data plots. Points on dark grey  
16 areas correspond to sampled cases where the categorical (Csub) and the geometric morphometric (GM) data  
17 sets disagree on which group is more disparate.  
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25 **Table 1.** Percentage variance summarized on the first three PCo axes for each of the three data sets.  
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28 **Table 2.** Correlation results between disparity and taxonomic diversity over time in osteostracans. Disparity  
29 is calculated as the preordination distance (PD) and as the ratio of generalized variance (GV). Taxonomic  
30 diversity is measured as the raw number of genera at each temporal interval (RD) and considering ghost  
31 ranges (GR) (data taken from Sansom *et al.* 2015). Asterisks denote results obtained after first-difference  
32 data transformation.  
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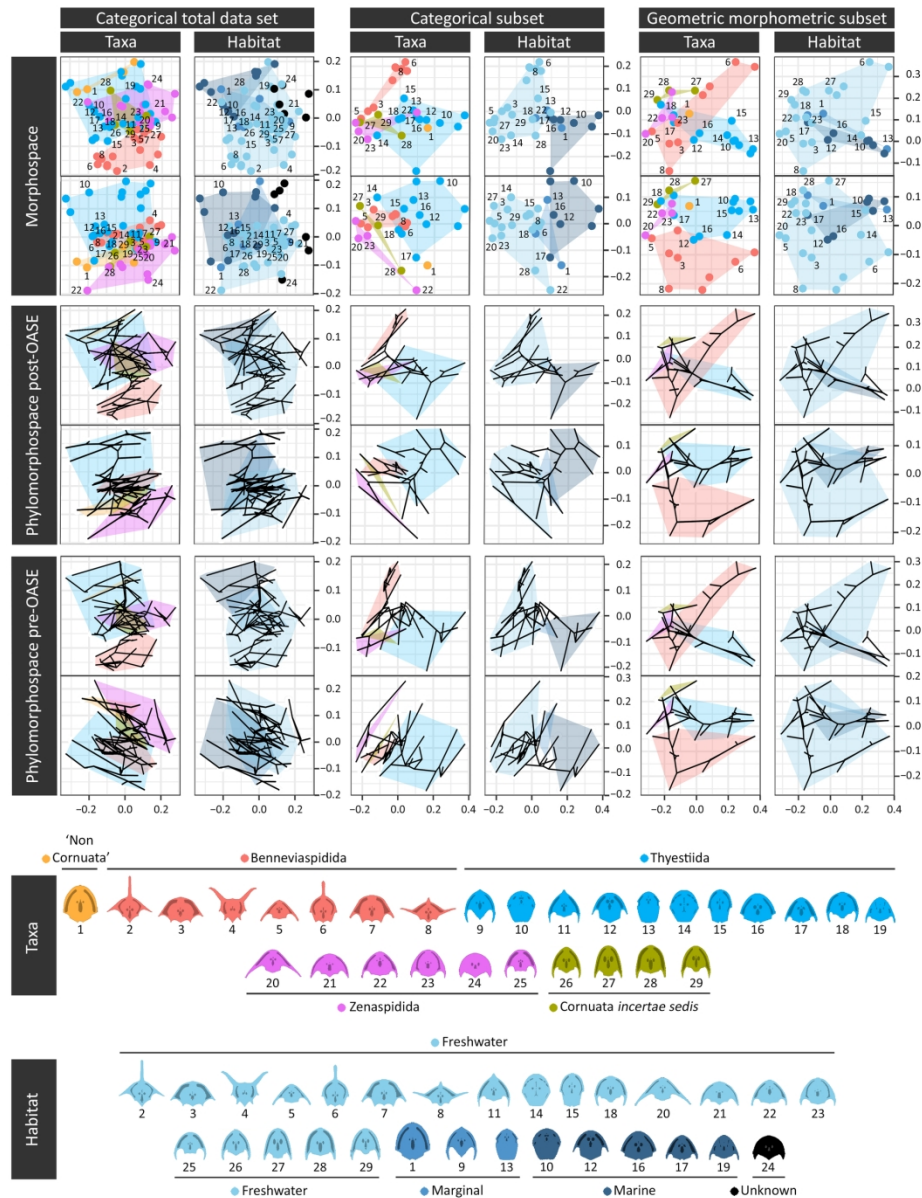
38 **Appendix S1.** List of genera and specimens used for categorical and geometric morphometric approaches.  
39 Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY, USA; MNHM,  
40 Museum National d'Histoire Naturelle, Paris, France; NHM, Natural History Museum, London, UK; OUM,  
41 Oxford University Museum of Natural History, Oxford, UK; PMO, Naturhistorisk Museum (Paleontologi),  
42 University of Oslo, Norway.  
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(A) Drawings illustrating the general morphology of two distinct well-known osteostracans (*Cephalaspis* and *Tremataspis*) in dorsal (d), lateral (l) and frontal views (f). Position of the pectoral fins (pf), dorsal fin (df), caudal fin (cf) and the headshield (hs) is indicated. (B) Descriptive diagrams showing the terminology of commonly referred anatomical characters of osteostracan headshield (upper diagram) and the landmark configuration used in the geometric morphometric analysis (lower diagram). Landmark 1, anterior tip of the headshield or the rostral process (ant. tip.); Landmark 2, posterior tip of the headshield (post. tip.); Landmarks 3 and 4, most anterior and most posterior medial points of the nasohypophysial opening (nas. op.) respectively; Landmark 5, pineal foramen (pi. f.); Landmarks 6 and 7, most anterior and most posterior medial points of the median field (m. fi.) respectively; Landmarks 8 and 9, most anterior points of the lateral fields (l. fi.); Landmarks 10 and 11, most posterior points of the lateral fields (l. fi.); Landmarks 12 and 13, points of connection between the headshield and the body; Landmarks 14 and 15, most distal points of the corneal processes (cor. pr.); Landmarks 16–23, most anterior, posterior, lateral and medial points of the eye orbits (ob.); Landmarks 24–73, landmarks situated between Landmarks 1 and 14 and between Landmarks 1 and 15; Landmarks 74–103, landmarks situated between Landmarks 14 and 12 and between Landmarks 15 and 13; Landmarks 104–123, landmarks situated between Landmarks 12 and 2 and between Landmarks 13 and 2. (C) Phylogenetic hypothesis of the Osteostraci (modified from Samson et al. 2015), highlighting in black the species represented in the geometric morphometric analysis.

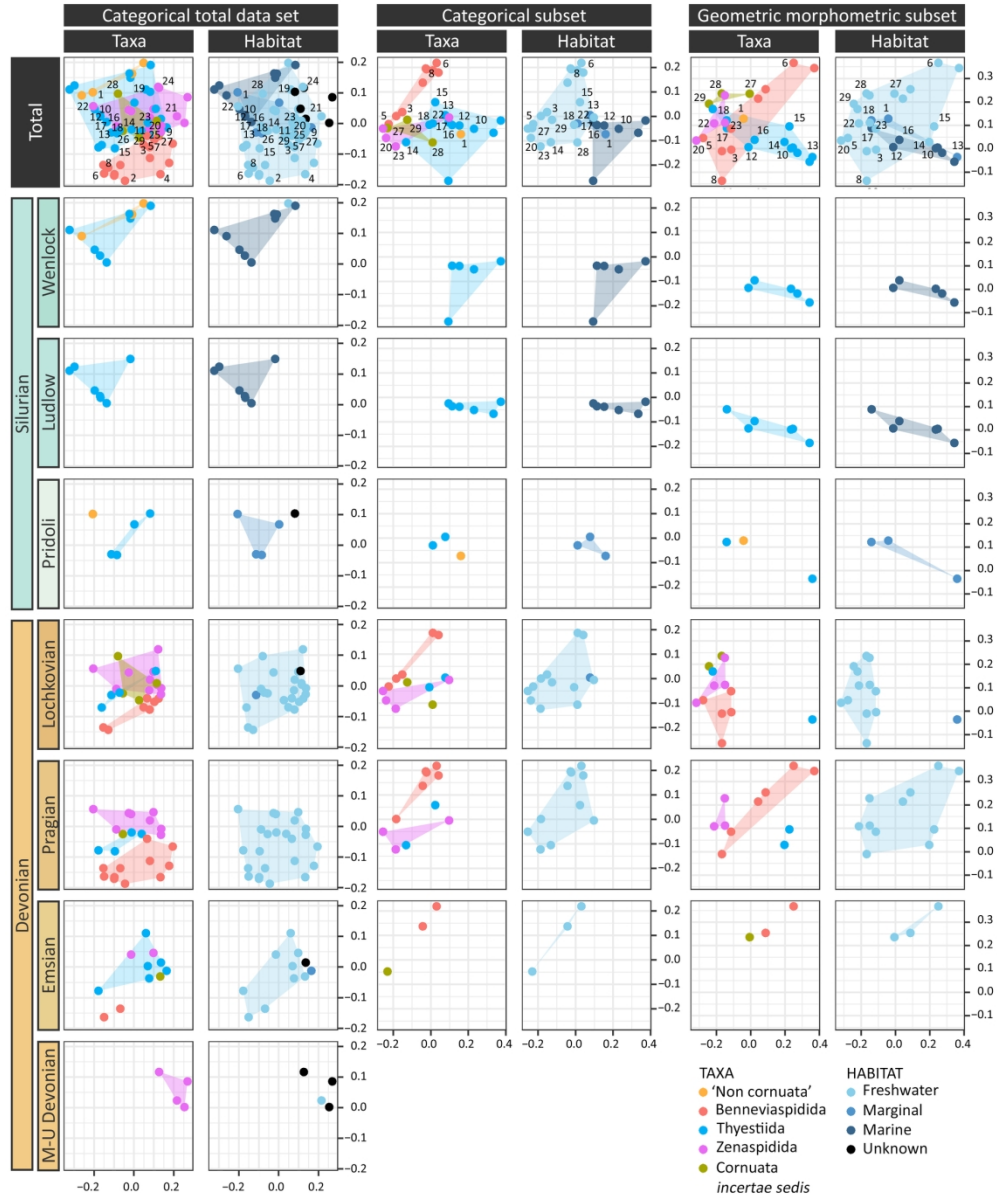
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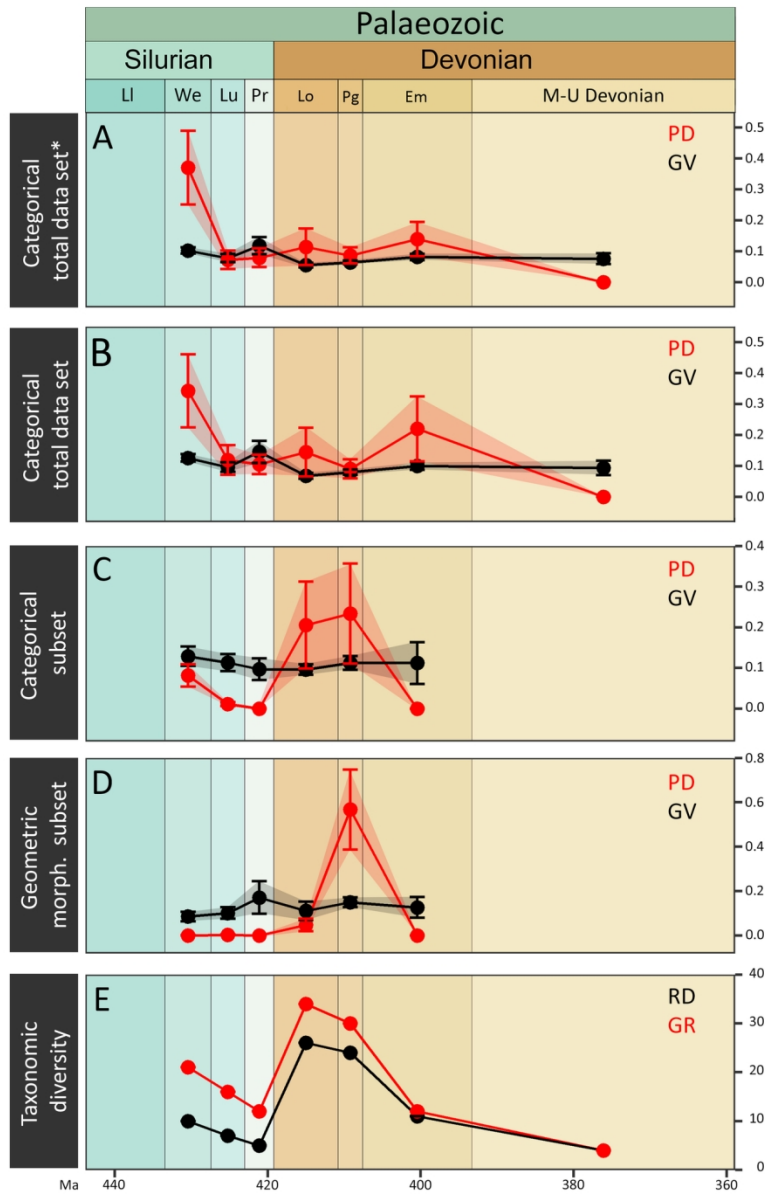
Morphospace occupation and phylomorphospaces of osteostracans grouped by major taxa and habitats obtained from categorical and geometric morphometric approaches. Morphospaces and phylomorphospaces are represented by PCo1 (horizontal), PCo2 (upper vertical) and PCo3 (lower vertical) axes. Osteostracan phylogenetic relationships and headshield drawings modified from Sansom (2009a). Taxa: 1, *Hemicyclaspis*; 2, *Boreaspis*; 3, "*Benneviaspis*" *lankesteri*; 4, *Tauraspis*; 5, *Ectinaspis*; 6, *Spatulaspis*; 7, "*Benneviaspis*" *longicornis*; 8, *Hoelaspis*; 9, *Camptaspis*; 10, *Oeselaspis*; 11, *Yvonaspis*; 12, *Thyestes*; 13, *Didymaspis*; 14, *Acrotomaspis*; 15, *Norselaspis*; 16, *Witaaspis*; 17, *Procephalaspis*; 18, *Waengsjoeaspis*; 19, *Ilemoraspis*; 20, *Stensiopelta*; 21, *Trewinia*; 22, *Zenaspis*; 23, *Tegaspis*; 24, *Escuminaspis*; 25, *Spangenhelmaspis*; 26, *Pattenaspis*; 27, *Hildenaspis*; 28, *Cephalaspis*; 29, *Mimetaspis*.

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Temporal patterns of morphospace occupation of osteostracans grouped by major taxa and habitats obtained from categorical and geometric morphometric approaches. Morphospaces are only represented by PCo1 (horizontal) and PCo2 (vertical) axes. Numbers in the morphospaces refer to taxa in Figure 2.

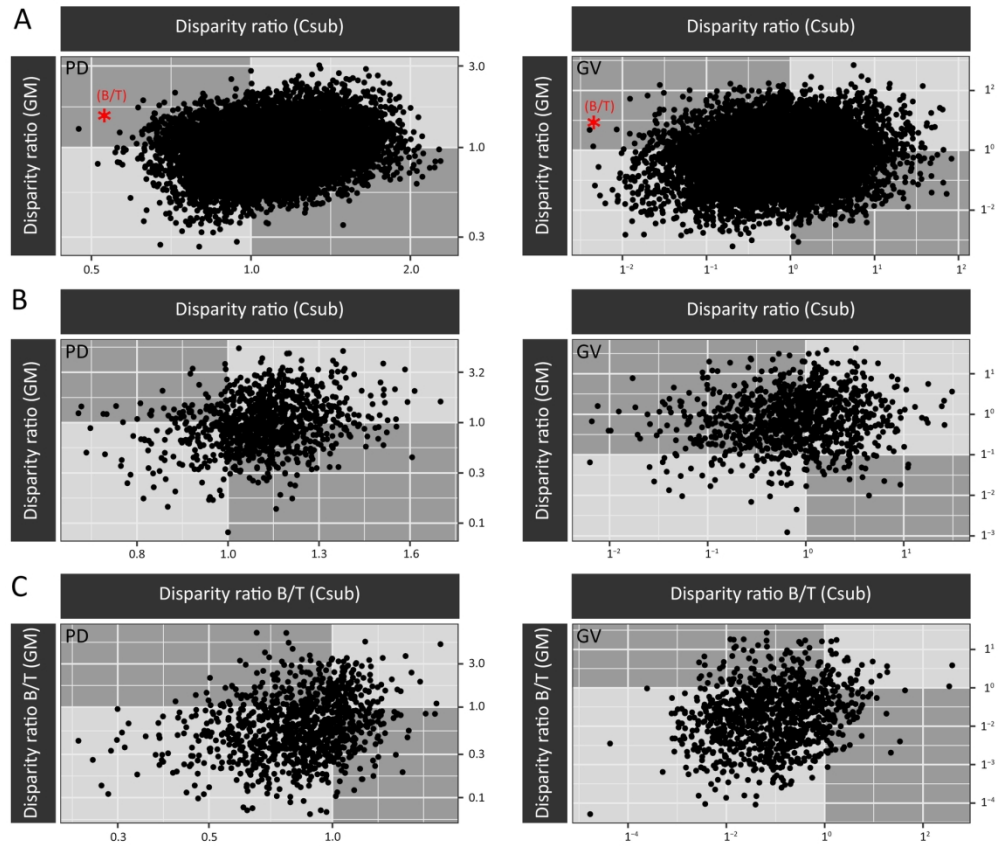
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A-C. Temporal patterns of morphological disparity obtained from categorical and geometric morphometric data calculated as the preordination distance (PD) and as the ratio of generalized variance (GV). Asterisk denote the categorical total data set including both corpal and headshield characters. Taxonomic diversity of osteostracans through time based on raw data (RD) and including ghost ranges (GR) (data taken from Sansom et al. 2015). *Timescale*: Ll, Llandovery; We, Wenlock; Lu, Ludlow; Pr, Pridoli; Lo, Lochkovian; Pg, Pragian; Em, Emsian; M-U Devonian, Middle-Upper Devonian.

110x171mm (300 x 300 DPI)





Plots showing the disparity ratios derived from the categorical (Csub) and the geometric morphometric (GM) data sets in both (A) the empirical and (B-C) the modelled approaches. Disparity is calculated as both the preordination distance (PD) and as the ratio of generalized variance (GV). The disparity ratios are calculated on two randomly selected groups of 9 and 12 taxa in (A) the empirical and (B) the modelled data as well as on *Benneviaspida* and *Thyestida* in (C) the modelled data. Actual ratio of *Benneviaspida* and *Thyestida* (B/T) is denoted by an asterisk in the empirical data plots. Points on dark grey areas correspond to sampled cases where the categorical (Csub) and the geometric morphometric (GM) data sets disagree on which group is more disparate.

166x140mm (300 x 300 DPI)

		Percentage variance summarized			
	<b>Data set</b>	Axis 1	Axis 2	Axis 3	Sum
4	Cladistic	19.11%	10.29%	7.58%	36.98%
5	Cladistic subset	27.45%	15.41%	9.85%	52.71%
6	Geometric morphometric	57.67%	18.99%	13.33%	89.99%

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		Cladistic	(GV)	Cladistic	(PD)
<b>Diversity</b>	<b>Pearson Correlation</b>		0.075		-0.694
(Raw data)	<b>Sig.</b>		<i>0.872</i>		<i>0.084</i>
<b>Diversity</b>	<b>Pearson Correlation</b>		0.260		-0.502
(Ghost ranges includ.)	<b>Sig.</b>		<i>0.574</i>		<i>0.251</i>
<b>Diversity*</b>	<b>Pearson Correlation</b>		0.141		-0.745
(Raw data)	<b>Sig.</b>		<i>0.789</i>		<i>0.089</i>
<b>Diversity*</b>	<b>Pearson Correlation</b>		0.077		-0.750
(Ghost ranges includ.)	<b>Sig.</b>		<i>0.884</i>		<i>0.086</i>

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<b>Cladistic Sub. (GV)</b>	<b>Cladistic Sub. (PD)</b>	<b>Geom. Morph. (GV)</b>	<b>Geom. Morph. (PD)</b>
0.946	-0.235	0.621	-0.011
<i>0.004</i>	<i>0.654</i>	<i>0.189</i>	<i>0.983</i>
0.968	-0.181	0.545	-0.181
<i>0.002</i>	<i>0.808</i>	<i>0.264</i>	<i>0.731</i>
0.946	0.064	0.419	-0.483
<i>0.015</i>	<i>0.918</i>	<i>0.408</i>	<i>0.410</i>
0.955	0.054	0.436	-0.452
<i>0.011</i>	<i>0.931</i>	<i>0.387</i>	<i>0.445</i>

List of genera and specimens used for categorical and geometric morphometric approaches.  
Museum, London, UK; OUM, Oxford University Museum of Natural History, Oxford, UK; PMU

Genera	Major taxa	Species in the cladistic (CD) data set
<i>Aceraspis</i>	NonCornuata	<i>Aceraspis robustus</i>
<i>Ateleaspis</i>	NonCornuata	<i>Ateleaspis tessellata</i>
<i>Hemicyclaspis</i>	NonCornuata	<i>Hemicyclaspis murchisoni</i>
<i>Hirella</i>	NonCornuata	<i>Hirella gracillis</i>
<i>Belonaspis</i>	Benneviaspida	<i>Belonaspis puella</i>
<i>Benneviaspis</i>	Benneviaspida	<i>Benneviaspis holtedahli</i>
" <i>Benneviaspis</i> "	Benneviaspida	" <i>Benneviaspis</i> " <i>anglica</i>
" <i>Benneviaspis</i> "	Benneviaspida	" <i>Benneviaspis</i> " <i>lankesteri</i>
" <i>Benneviaspis</i> "	Benneviaspida	" <i>Benneviaspis</i> " <i>longicornis</i>
<i>Boreaspis</i>	Benneviaspida	<i>Boreaspis rostrata</i>
" <i>Boreaspis</i> "	Benneviaspida	" <i>Boreaspis</i> " <i>ceratops</i>
" <i>Boreaspis</i> "	Benneviaspida	" <i>Boreaspis</i> " <i>intermedia</i>
<i>Dicranaspis</i>	Benneviaspida	<i>Dicranaspis gracilis</i>
<i>Ectinaspis</i>	Benneviaspida	<i>Ectinaspis heintzi</i>
<i>Hapilaspis</i>	Benneviaspida	<i>Hapilaspis apheles</i>
<i>Hoelaspis</i>	Benneviaspida	<i>Hoelaspis angulata</i>
<i>Securiaspis</i>	Benneviaspida	<i>Securiaspis kitchini</i>
<i>Severaspis</i>	Benneviaspida	<i>Severaspis rostralis</i>
<i>Spatulaspis</i>	Benneviaspida	<i>Spatulaspis costata</i>
<i>Tauraspis</i>	Benneviaspida	<i>Tauraspis rara</i>
<i>Acrotomaspis</i>	Thyestida	<i>Acrotomaspis instabilis</i>
<i>Aestiaspis</i>	Thyestida	<i>Aestiaspis wiitaensis</i>
<i>Auchenaspis</i>	Thyestida	<i>Auchenaspis salteri</i>
<i>Axinaspis</i>	Thyestida	<i>Axinaspis whitei</i>
<i>Camptaspis</i>	Thyestida	<i>Camptaspis utahensis</i>
<i>Dartmuthia</i>	Thyestida	<i>Dartmuthia gemmifera</i>
<i>Didymaspis</i>	Thyestida	<i>Didymaspis grindrodi</i>
<i>Gustavaspis</i>	Thyestida	<i>Gustavaspis trinodis</i>
<i>Ilemoraspis</i>	Thyestida	<i>Ilemoraspis kirkinskayae</i>
<i>Kiaeraspis</i>	Thyestida	<i>Kiaeraspis auchenaspidoides</i>
<i>Nectaspis</i>	Thyestida	<i>Nectaspis areolata</i>
<i>Norselaspis</i>	Thyestida	<i>Norselaspis glacialis</i>
<i>Oeselaspis</i>	Thyestida	<i>Oeselaspis pustulata</i>
<i>Procephalaspis</i>	Thyestida	<i>Procephalaspis oeselensis</i>
<i>Saaremaspis</i>	Thyestida	<i>Saaremaspis mickwitzii</i>
<i>Sclerodus</i>	Thyestida	<i>Sclerodus pustuliferus</i>
<i>Tannuaspis</i>	Thyestida	<i>Tannuaspis levenkoi</i>
<i>Thyestes</i>	Thyestida	<i>Thyestes verrucosus</i>
<i>Timanaspis</i>	Thyestida	<i>Timanaspis kossovoi</i>
<i>Tremataspis</i>	Thyestida	<i>Tremataspis schrenkii</i>
<i>Tyriaspis</i>	Thyestida	<i>Tyriaspis whitei</i>
<i>Waengsjoeaspis</i>	Thyestida	<i>Waengsjoeaspis excellens</i>
<i>Witaaspis</i>	Thyestida	<i>Witaaspis schrenkii</i>
<i>Yvonaspis</i>	Thyestida	<i>Yvonaspis cambelltonensis</i>
<i>Dobraspis</i>	Thyestidaa	<i>Dobraspis uralensis</i>
<i>Balticaspis</i>	Zenaspida	<i>Balticaspis latvica</i>
<i>Diademaspis</i>	Zenaspida	<i>Diademaspis poplinae</i>
<i>Escuminaspis</i>	Zenaspida	<i>Escuminaspis laticeps</i>

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2	<i>Levesquaspis</i>	Zenaspida	<i>Levesquaspis patteni</i>
3	<i>Machairaspis</i>	Zenaspida	<i>Machairaspis crystis</i>
4	<i>Parameteoraspis</i>	Zenaspida	<i>Parameteoraspis gigas</i>
5	<i>Scolenaspis</i>	Zenaspida	<i>Scolenaspis signata</i>
6	<i>Spangenhelmaspis</i>	Zenaspida	<i>Spangenhelmaspis staxrudi</i>
7	<i>Stensiopelta</i>	Zenaspida	<i>Stensiopelta woodwardi</i>
8	<i>Superciliaspis</i>	Zenaspida	<i>Superciliaspis gabrielsei</i>
9	<i>Tegaspis</i>	Zenaspida	<i>Tegaspis kollerii</i>
10	<i>Trewinia</i>	Zenaspida	<i>Trewinia magnifica</i>
11	<i>Ukrainaspis</i>	Zenaspida	<i>Ukrainaspis kozlowski</i>
12	<i>Wladysagitta</i>	Zenaspida	<i>Wladysagitta janvieri</i>
13	<i>Zenaspis</i>	Zenaspida	<i>Zenaspis salweyi</i>
14	<i>Cephalaspis</i>	CornuataIncSed	<i>Cephalaspis lyelli</i>
15	<i>Hildenaspis</i>	CornuataIncSed	<i>Hildenaspis digitalis</i>
16	<i>Mimetaspis</i>	CornuataIncSed	<i>Mimetaspis hoeli</i>
17	<i>Pattenaspis</i>	CornuataIncSed	<i>Pattenaspis acuminata</i>
18	<i>Zychiaspis</i>	CornuataIncSed	<i>Zychiaspis siemiradzki</i>
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. Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY, US  
 O, Naturhistorisk Museum (Paleontologi), University of Oslo, Norway.

<b>Species in the geometric morphometric (GM) data set</b>	<b>Specimen number (for GM analysis)</b>	<b>Location</b>
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<i>Hemicyclaspis murchisoni</i>	P8811	NHM
-	-	-
<i>Belonaspis puella</i>	10811I	MNHM
<i>Benneviaspis holtedahli</i>	29879	PMO
-	-	-
<i>Benneviaspis lankesteri</i>	4687	NHM
-	-	-
<i>Boreaspis macrorhynchus</i>	29829	PMO
-	-	-
-	-	-
<i>Dicranaspis gracilis</i>	33578(277)	PMO
<i>Ectinaspis heintzi</i>	P40173	NHM
-	-	-
<i>Hoelaspis angulata</i>	24896	PMO
<i>Securiaspis kitchini</i>	P4115	NHM
-	-	-
<i>Spatulaspis robustus</i>	P54492(42)a	NHM
-	-	-
<i>Acrotomaspis instabilis</i>	P54412(415a)	NHM
-	-	-
<i>Auchenaspis egertoni</i>	P6112	NHM
-	-	-
-	-	-
<i>Dartmuthia gemmifera</i>	P24990	NHM
<i>Didymaspis grindrodi</i>	30486	OUM
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<i>Norselaspis glacialis</i>	1027	MNHM
<i>Oeselaspis pustulata</i>	9221	AMNH
<i>Procephalaspis oeselensis</i>	12972	AMNH
<i>Saaremaspis mickwitzi</i>	11423(T283)-9551	AMNH
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-	-	-
<i>Thyestes verrucosus</i>	12770	AMNH
-	-	-
<i>Tremataspis schmidtii</i>	P60567-12157	NHM
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<i>Waengsjoeaspis excellens</i>	P54347(518a)	NHM
<i>Witaaspis schrenkii</i>	11226-12714	AMNH
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7	<i>Stensiopelta pustulata</i>	P20554	NHM
8	-	-	-
9	<i>Tegaspis kolleri</i>	P40198	NHM
10	-	-	-
11	-	-	-
12	<i>Wladysagitta janvieri</i>	P9763	NHM
13	<i>Zenaspis salweyi</i>	P19227	NHM
14	<i>Cephalaspis lyelli</i>	P6945	NHM
15	<i>Hildenaspis</i> sp.	1166	MNHM
16	<i>Mimetaspis hoeli</i>	30046	PMO
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5 **Deformation**

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46 Slight deformation of the back of the head shield

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- 16 Possibly some but confined to the non-digitigez side of the head shield
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