

Testing for taphonomic bias in deep time using trilobite sclerite ratios



Jonathan M. Adrain^a, Stephen R. Westrop^{b,*}

^a Department of Earth and Environmental Sciences, University of Iowa, Iowa City, IA 52242, USA

^b Oklahoma Museum of Natural History and School of Geology and Geophysics, University of Oklahoma, Norman, OK 73072, USA

ARTICLE INFO

Article history:

Received 28 July 2016

Received in revised form 10 October 2016

Accepted 12 October 2016

Available online 14 October 2016

Keywords:

Taphonomy

Trilobita

Ordovician

Sclerite sorting

ABSTRACT

Taphonomic sorting can be assessed directly in fossil assemblages by comparing expected and observed proportions of elements of multielement skeletons. Trilobites are model organisms for this approach because each individual possesses one cranidium (head) and one pygidium (tail). Departures from an expected 1:1 cranidia:pygidia (C/P) ratio reflect taphonomic processes such as size- or shape-sorting. We analyzed a dataset of >16,000 secondarily silicified cranidia and pygidia from subtidal, storm-influenced facies of a highstand systems tract in the House Limestone (Lower Ordovician) in Utah. Species fall into four distinct isotaphonomic groups, which we define as sets of morphologically similar species likely to have similar responses to taphonomic processes. All isotaphonomic groups have median C/P ratios that depart significantly from expected proportions; micropygous groups show strong enrichment of cranidia in all samples, whereas isopygous groups include some pygidia-rich samples. Despite this, rank orders of abundances and C/P ratios are not correlated for any isotaphonomic group, indicating that sorting bias is not controlling abundance patterns. Cluster analysis of genus abundance data defined two biofacies, each of which included unique dominant taxa, and which characterized early and late highstand strata. The same groupings of samples were readily recognizable using ordination (non-metric multidimensional scaling). Rank orders of C/P and positions of samples along ordination axes are not correlated, so that sorting bias does not influence biofacies groupings. Rank order of species richness of samples, both before and after rarefaction also shows no correlation with C/P. The results indicate that paleoecological analysis is possible despite clear evidence of taphonomic sorting. In this case, sorting has shuffled sclerite ratios without having a significant impact on taxon abundances and species richness. However, taphonomic bias may be problematic in more proximal marine environments where frequent winnowing produces extensive sorting and differential breakage of skeletal material.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

The overwhelming majority of marine fossil assemblages are accumulations of shells that have been concentrated to varying degrees by hydrodynamic processes or by low rates of background sedimentation. Intuitively, we expect depositional processes to influence parameters such as taxon abundance and richness, which underpin most paleoecological and paleobiological studies. That is, taxon abundance in the fossil record is a reflection of original ecologic abundance filtered by taphonomic processes (including hydrodynamic size and shape sorting of shells or sclerites, and differential breakage). Implicit in any analysis of fossil abundance data is the assumption that taphonomic overprint is sufficiently low that comparisons between samples yield meaningful ecological patterns, or that taphonomically distorted collections can at minimum be identified and accounted for (e.g., Westrop, 1986).

Estimating the extent to which taphonomy has altered original abundance is, however, difficult, and most work has focused on

actualistic studies of Recent life and death assemblages (e.g., Alin and Cohen, 2004; Edinger et al., 2001; Greenstein, 1993; Kidwell, 2001, 2002, 2013; Lockwood and Chasant, 2006; Olszewski and Kidwell, 2007; Tomašových, 2006; Tomašových and Kidwell, 2009). The results of these studies are generally optimistic in outlook. They indicate that at least in modern molluscan-dominated faunas and at coarse mesh sizes, death assemblages on average retain much of the taxon-abundance information of their source communities. However, moving beyond the surficial record of unconsolidated sediment in modern environments is a challenge, and the extent to which live-dead comparisons can be extrapolated back to what are likely more strongly filtered assemblages in the fossil record is far from clear.

In deep time, we lack the base line of live abundances for comparison, so that bias must be assessed indirectly. Comparative field studies can be informative where analogues of modern molluscan assemblages are preserved. Tomašových (2006), for example, used ordinations of non-reworked vs. storm-reworked, bivalve-rich, Triassic shell beds to show that fidelity was not substantially affected by storm reworking. An alternative approach compares expected and observed abundances of skeletal elements to identify taphonomic overprint of abundance

* Corresponding author.

E-mail address: swestrop@ou.edu (S.R. Westrop).

data (Moore and Norman, 2009). This method exploits the fact that the number of skeletal elements contributed to the fossil record by each individual is usually known, and departures from expected proportions will indicate taphonomic sorting or differential destruction.

In this paper we combine these methods in a comprehensive, field-based analysis of taphonomic bias in a Lower Ordovician trilobite fauna. We use sclerite ratios to test for taphonomic bias in the abundances of groups of species within samples, and examine the differential response of various morphotypes to shared depositional processes. We also apply multivariate methods to define groupings of samples (biofacies or trilobite communities) and test for a relationship between these groupings and sclerite ratios.

2. Trilobites as model organisms for studying taphonomic bias

Trilobites were diverse and widespread components of Lower Paleozoic marine communities. Their remains occur in virtually all sedimentary facies, from peritidal carbonates to shales and carbonates deposited in slope or deep basinal settings (e.g., Fortey, 1975; Westrop and Adrain, 1998). This broad distribution, together with their multielement skeletons, makes trilobites model organisms for investigation of taphonomic patterns.

Analysis of multi-element skeletons offers a novel way to assess taphonomic bias and fidelity of fossil assemblages (Moore and Norman, 2009). All trilobites have a single cranidium (head) and pygidium (tail), usually of quite different size and shape. Regardless of age, environment or taxon, they entered the sedimentary record with an initial cranidia: pygidia (C/P) ratio of 1, and any departure from this will reflect post-mortem processes. Trilobite sclerite ratios in fossil samples hold the promise of a powerful means to test for taphonomic overprint. They are potentially more sensitive indicators of taphonomic overprint than those of other, mostly bivalved invertebrates because trilobites encompass a far wider range of morphological diversity. Distinct morphotypes recur repeatedly through the history of trilobites and have been studied extensively for the interpretation of life habits (e.g., Westrop, 1983; Fortey and Owens, 1990, 1997). These morphotypes can also be exploited in comparative taphonomic studies. Studies in vertebrate paleontology have traditionally made comparisons between samples that deemed to be isotaphonomic, either by showing similar taphonomic attributes, or by being drawn from similar depositional environments likely to have experienced similar taphonomic processes (e.g., Behrensmeier et al., 1992; Moore and Norman, 2009). In this paper, we coin the term

“isotaphonomic group” to describe sets of species with similar morphologies that can be expected to respond in similar ways to waves and currents. Isotaphonomic groups incorporate measures of both size and shape. They may be isopygous (cranidium and pygidium similar in size), strongly micropygous (in which the pygidium is much smaller than the cranidium), or in some cases macropygous (with the pygidium larger than the cranidium). They range from strongly vaulted to nearly flat, or from spiny or tuberculate to almost completely smooth. As such, they are conceptually similar to the morphotypes of Fortey and Owens (1990, 1997). Typical trilobite assemblages are composed of several isotaphonomic groups, permitting comparison of sorting patterns both within and between groups. In fact, trilobites are sufficiently diverse in morphology to act as proxies for community-wide patterns. They have the advantage of controlling for other sources of variation, including differences in shell composition, microstructure and in the nature of the articulation between skeletal components, which complicate sorting in, for example, rhynchonelliform brachiopods (Alexander, 1990).

3. Stratigraphic setting

3.1. Study area

The study area, in the Ibex area of the southern House Range, Millard County, western Utah (Fig. 1), has a long history of research and exposes one of the classic Lower Ordovician successions in North America (e.g., Hintze, 1953; Ross et al., 1997; Adrain et al., 2009, 2014). The oldest Ordovician unit in the southern House Range is the House Limestone, a carbonate succession that has been divided into three members by Miller et al. (2001). We sampled the youngest of these, the Red Canyon Member, in a 69.5 m segment of the upper half of a measured section at the Lava Dam North locality (Fig. 1B) documented most recently by Miller et al. (2001, 2003) and Adrain et al. (2003).

3.2. Sedimentary facies and sequence stratigraphy

The Lower Ordovician sequence stratigraphy and sedimentary facies of the study area will be treated elsewhere, and only a brief summary is presented here. Most of the Red Canyon Member has been interpreted as a highstand succession above lowstand to transgressive systems tracts recorded by the underlying Burnout Canyon Member (Miller et al., 2003; Saltzman et al., 2015). The entire member has been assigned to the *Rossodus manitouensis* (conodont) Zone (Miller et al., 2003),

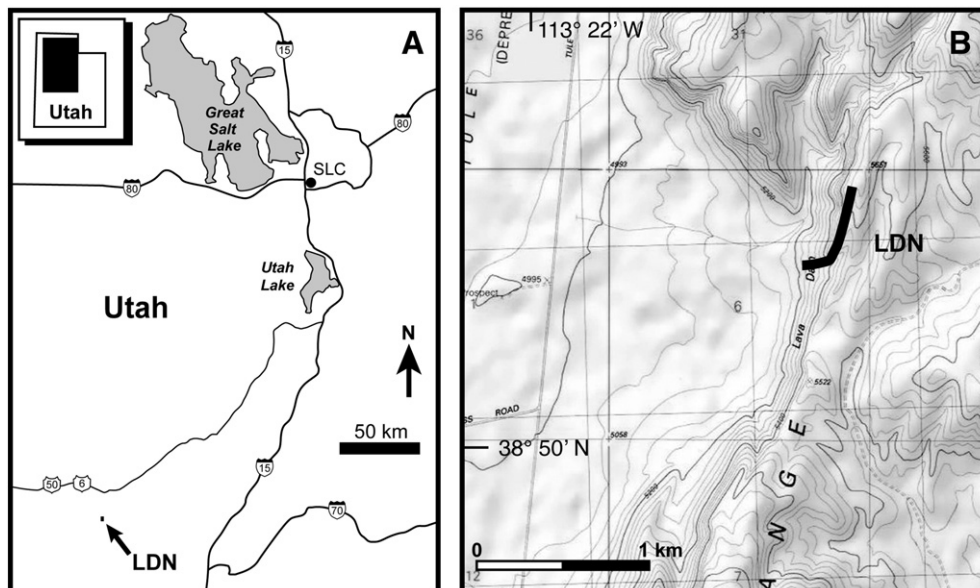


Fig. 1. Maps showing the location of section LDN (Lava Dam North).

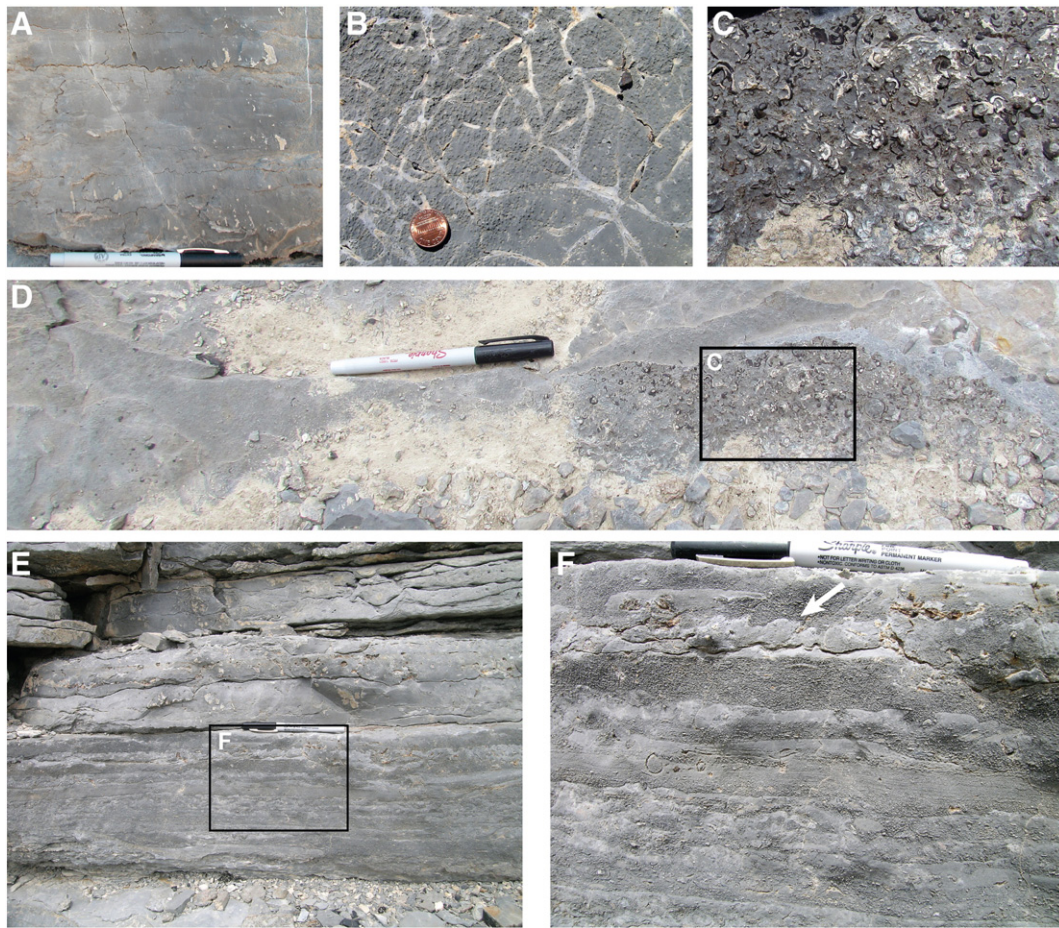


Fig. 2. Lithofacies of the Red Canyon Member of the House Formation at section LDN. **A.** Bioturbated, stylolitic lime mudstone-wackestone. **B.** Horizontal burrows in lime mudstone-wackestone. **C.** Thin (mm-thick), dense concentration of mostly hintzecurine heads as a veneer on a bedding surface. **D.** Sorting of sclerites on a decimeter scale produces patchy distributions: concentration of heads shown in Fig. C (rectangle) passes laterally into a sparsely fossiliferous area. **E.** Cycle from the upper Red Canyon comprising a lower interval of heterolithic facies and an upper interval of bioturbated lime mudstone-wackestone; contact between intervals at pen. Rectangle shows portion of heterolithic facies enlarged in Fig. 2F. **F.** Heterolithic facies showing cm-thick layers of lime mudstone to wackestone, laminated calcisiltite and bio-intraclastic pack- and grainstone. Layers are separated by sub-planar, gently undulating to irregular (white arrow) scoured surfaces.

indicating that it lies within the lower Tremadocian Stage (upper Skullrockian Stage of the North American nomenclature).

Two lithofacies dominate the Red Canyon Member. The bioturbated lime mudstone-wackestone facies (Fig. 2A, B) also includes minor cm- to dm-thick intraclastic rudstone layers and dm-thick intervals of calcisiltite; thin (mm-thick), patchy accumulations of silicified trilobites sclerites occur on some bedding surfaces (Fig. 2C, D) and these are the primary sources of the samples used in this study. The lithofacies occurs

throughout the succession, but accounts for most of the early highstand (lower 45 m of the study interval). It is interpreted as recording subtidal deposition above mean storm wave base.

The late highstand (upper 24 m of the study interval) is characterized by the addition of the heterolithic facies (Fig. 2E, F), which is composed of cm- to dm-thick layers of lime mudstone-wackestone, calcisiltite, and bio-intraclastic packstone, grainstone and rudstone. Boundaries between layers are subplanar to irregular scoured surfaces

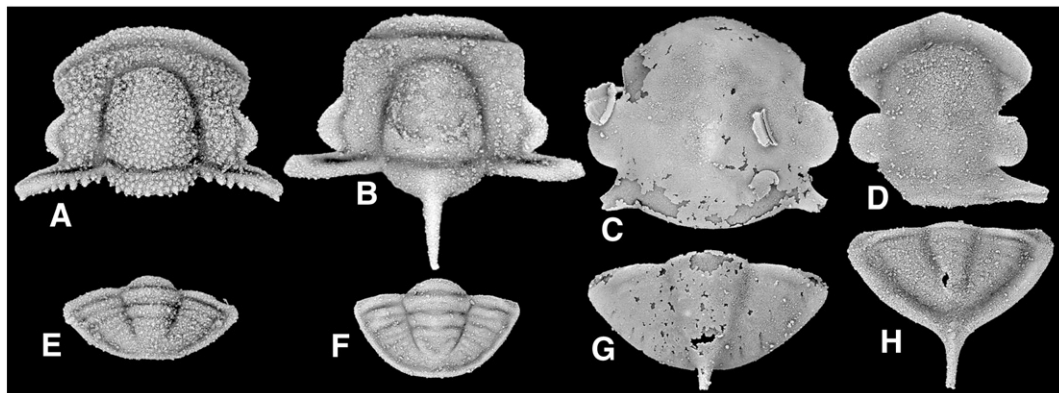


Fig. 3. Cranidia and pygidia of isotaphonomic groups. **A, E,** cranidium and pygidium of Hintzecurinae (Group 1). **B, F,** cranidium and pygidium of *Politicus* (Group 2). **C, G,** cranidium and pygidium of *Symphysurina* (Group 3). **D, H,** cranidium and pygidium of Asaphidae (Group 4).

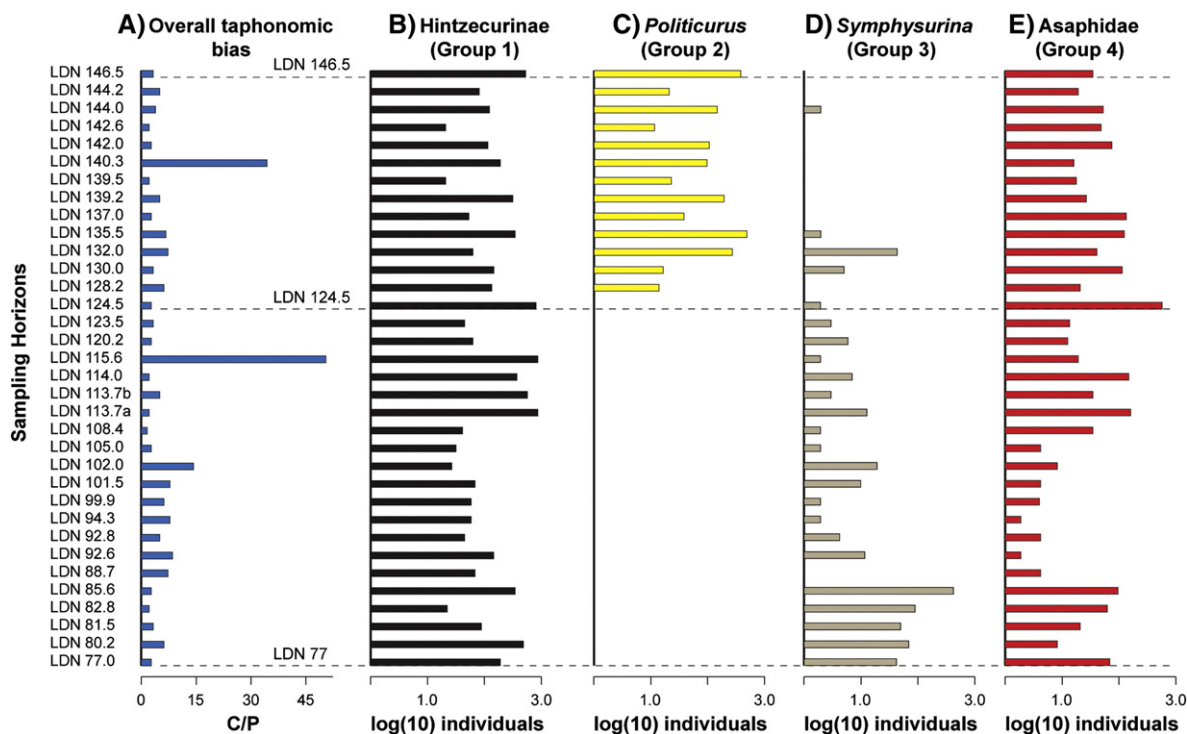


Fig. 4. Collection data from Section Lava Dam North; collections are stacked in ascending stratigraphic order. Sample numbers indicate meters above the base of the section, with the base of the Red Canyon Member at 77.0 m). **A.** Overall taphonomic bias in collections, expressed as the cranidia:pygidia (C/P) ratio for each entire sample; there is no correlation between stratigraphic order and rank order of C/P (Spearman's rho, 0.118; $p = 0.51$). **B–E.** Relative abundance of each isotaphonomic group (Fig. 3) expressed as $\log_{10}$ abundance of individuals in collections. **B.** Hintzeturinae (Group 1). **C.** *Politicurus* (Group 2). **D.** *Symphysurina* (Group 3). **E.** Asaphidae (Group 4).

(Fig. 2F), at least some of which are hardgrounds; thin accumulations of trilobites are present. Heterolithic facies of this kind have been interpreted as recording deposition in a shallow subtidal to intertidal setting (e.g., Pratt, 2010), but the presence of diverse trilobite faunas (up to eleven species) argues for a subtidal, rather than intertidal, origin. It does, however, represent a shallower setting than the bioturbated lime mudstone–wackestone facies.

The late highstand is characterized by meter-scale, cyclic alternations of the heterolithic and lime mudstone–wackestone facies (Fig. 2E); at least nine cycles are present in the study interval. They could be interpreted as conventional, shallowing upward parasequences that are capped by heterolithic facies. However, boundaries between hemicycles are sharp and non-gradational (Fig. 2E), suggesting that they may be better regarded as high-frequency sequences (e.g., Zecchin and Catuneanu, 2013). The heterolithic facies forms the base of each cycle, recording a small-scale TST, with the lime mudstone–wackestone facies recording the highstand. From this perspective, the cycles are largely deepening upward.

The highstand succession of the Red Canyon Member follows the expected pattern with shallowing in the latter part (normal regression) as sedimentation fills accommodation space. Trilobites are present throughout the member and, as discussed below, the general shallowing trend may have some relevance for the interpretation of the abundances of isotaphonomic groups (Figs. 3, 4B–E) and the distribution of biofacies. However, there is no correlation between stratigraphic order of samples and the rank order of the overall C/P ratio of samples (Fig. 4A), so that there was no change in sorting regime through the overall shallowing between early and late highstand. In addition, there is no correlation between the rank orders of sample size and C/P ratio (Fig. 5).

4. Methods

The Lower Ordovician succession at Ibex is well known for secondary silicification of trilobite sclerites (e.g., Hintze, 1953; Adrain et al.,

2003, 2009, 2012, 2014; McAdams and Adrain, 2011a, 2011b, 2011c). Horizons in the carbonates of Red Canyon Member with silicified trilobites were discovered by searching for sclerites weathering out in relief on bedding and other surfaces; every bed in the member that showed evidence of silicification was sampled. Beyond the likelihood of silicification, details of taphonomic attributes (fragmentation, sorting) or taxon abundances were not evident in the field. Rather, the preservational condition of sclerites and taxonomic composition of each sample were revealed following processing by dissolution of limestone matrix in dilute hydrochloric acid. There was no conscious bias towards collecting samples of a particular taphonomic grade in the field.

Abundance counts were made using the minimum number of individuals (MNI) method (Gilinsky and Bennington, 1994), which in practice meant the maximum of either cranidia or pygidia for each species in the sample. These sclerites can be identified readily, whereas others

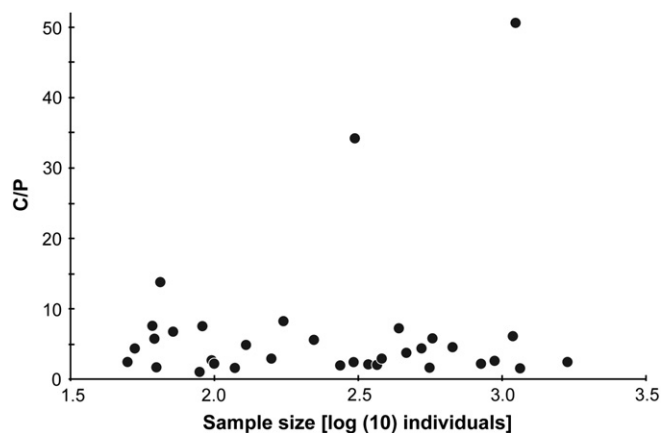


Fig. 5. Plot of overall taphonomic bias, expressed as the cranidia:pygidia (C/P) ratio, against sample size (individuals). Rank order of C/P ratio is not correlated with sample size (Spearman's rho = -0.076 ; $p = 0.67$).

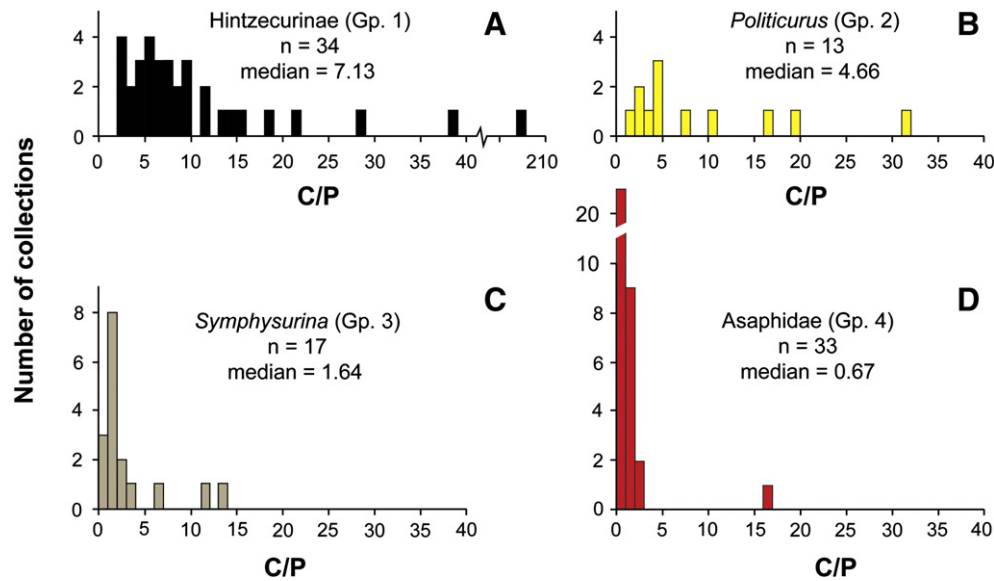


Fig. 6. Frequency distributions of crania:pygidia (C/P) ratios for isotaphonomic group. **A.** Hintzeturinae (Group 1). **B.** *Politicus* (Group 2). **C.** *Symphysurina* (Group 3). **D.** Asaphidae (Group 4). Aside from Group 1 versus Group 2, all pair-wise comparisons are significantly different with both a Mann-Whitney *U* test and a Kolmogorov-Smirnov test (Table 1).

(e.g., hypostomes) are more difficult to assign to species, and counts of isolated thoracic segments cannot be converted with confidence into individuals. Because trilobites molt, it is conceivable although unlikely that an individual trilobite contributed more than one set of sclerites to an assemblage. Molt frequency declines in mature individuals of many modern aquatic arthropods, and there may be a terminal molt (e.g., Havens and McConaughy, 1990; Walls et al., 2002; Tamone et al., 2007); the distribution of pre-mortem epibionts in *Flexicalymene* indicates that this was also the case in trilobites (Brandt, 1996). Moreover, preservation potential of small sclerites of earlier instars will be relatively low, so that it seems likely that trilobite assemblages with different size classes for species record multiple generations, rather than the cumulative record of instars of a single generation. As such, typical trilobite assemblages may be little different from samples of invertebrates that grow by accretion.

Counts were restricted to mature (holaspid) sclerites. Immature (late meraspis; earlier ontogenetic stages are absent) pygidia were identified readily from the presence of proto-thoracic segments. Crania lack such obvious morphological identifiers, but articulated exoskeletons are known for all taxa, either from our collections or from elsewhere, and this allows relative sizes of holaspisid crania and pygidia to be determined. Eight small samples with fewer than 50 individuals were excluded from the analysis. This left 34 samples (Fig. 4) with a median size of 290 individuals, and a combined total of > 16,000 individuals; average stratigraphic spacing was 2.04 m, with a minimum of 0.2 m and a maximum of 4.6 m. Thirty-one of the samples are from the bioturbated lime mudstone–wackestone facies (26 from the lime mudstone–wackestones themselves and five from interlayered dm-thick calcisiltite units) and only three (LDN 132, 140.3 and 142.0) are from the heterolithic facies. Statistical analyses were performed with PAST v. 3.11 for the Macintosh (Hammer et al., 2001); sample sizes were log transformed ($\log_{10} n + 1$) prior to analysis to reduce the impact of extreme values.

For the analysis of taphonomic bias among morphotypes, species were divided into four readily identifiable isotaphonomic groups defined by sclerite shape, size and sculpture. Group 1 (Hintzeturinae; Fig. 3A) consists of small, vaulted, micropygous, and heavily tuberculate species. Group 2 (*Politicus*; Fig. 3B) comprise moderate to large sized species that are vaulted, micropygous, and smooth. Species of group 3 (*Symphysurina*; Fig. 3C) are large, nearly isopygous, vaulted, and smooth. Group 4 (Asaphidae; Fig. 3D) is also composed of large, isopygous and smooth species that differ from Group 3 in having flattened, rather than vaulted, sclerites.

5. Analysis of isotaphonomic groups

5.1. Sorting patterns among isotaphonomic groups and their relationships to abundance

All four isotaphonomic groups depart from the expected C/P ratio of 1.0 (Fig. 6) indicating some degree of sorting bias. The two micropygous groups (1, Hintzeturinae and 2, *Politicus*) show strong enrichment of crania, and pygidia-rich samples are absent (Fig. 6A, B). Median values differ between the two groups, but not significantly so (Table 1), suggesting the primary signal is sorting by relative size rather than shape. As would be anticipated, frequency distributions for the two isopygous groups (3, *Symphysurina*; 4, Asaphidae) are significantly different from those of the micropygous groups (Table 1). In both cases, C/P ratios are closer to the expected values (Fig. 6C, D), and include pygidia-rich samples. The median value is lower (<1) for Asaphidae than in *Symphysurina*, and this difference is significant (Table 1) indicating that the sorting patterns of isopygous taxa are unlikely to be the result of sclerite size alone. Rather, convexity likely plays a role, with the vaulted sclerites of *Symphysurina* behaving differently from the flattened sclerites of Asaphidae.

Despite clear evidence of taphonomic bias and differences in sorting patterns between isotaphonomic groups, there is no significant correlation between rank order of C/P and rank order of abundance for any of

Table 1

Test statistics and significance levels (bold) for all pair-wise comparisons of frequency distributions of crania:pygidia ratio for four isotaphonomic groups, using Mann-Whitney *U* (M-W) and Kolmogorov-Smirnov (K-S) tests.

	Group 1 M-W	Group 2 M-W	Group 3 M-W	Group 1 K-S	Group 2 K-S	Group 3 K-S
Group 2 M-W	195.5; 0.55					
Group 3 M-W	69; 0.0001	31.5; 0.001				
Group 4 M-W	32.5; 0.0001	13; 0.0001	113.5; 0.0006			
Group 2 K-S				0.27; 0.40		
Group 3 K-S				0.73; 0.0001	0.61; 0.004	
Group 4 K-S				0.91; 0.0001	0.91; 0.0001	0.55; 0.001

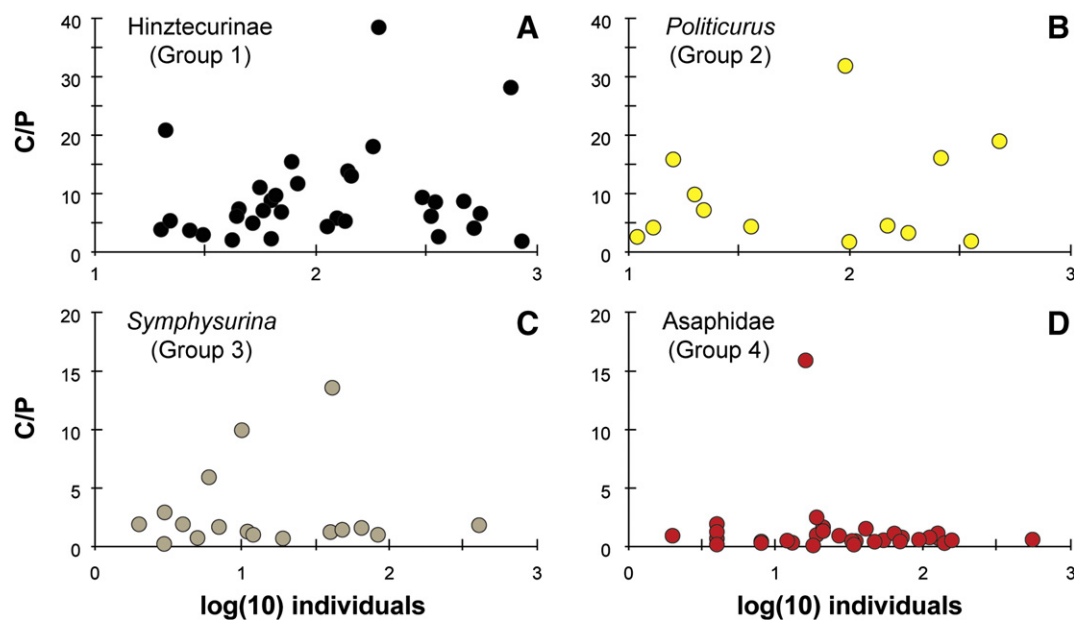


Fig. 7. Plots of abundances ($\log_{10}$ individuals) of isotaphonomic groups against their cranidia:pygidia (C/P) ratios for each collection. **A.** Hintzeturinae (Group 1). **B.** *Politicurus* (Group 2). **C.** *Symphysurina* (Group 3). **D.** Asaphidae (Group 4). One extreme outlier (C/P, 208; $\log_{10}$ abundance, 2.9211) is omitted from the Hintzeturine plot (A) to improve clarity, but was included in the calculation of rank correlation. For each of the four groups, there is no correlation between rank orders of abundance and C/P ratio (Table 2).

the groups (Fig. 7; Table 2). The MNI method of calculating number of individuals will tend to insulate abundance counts against simple taphonomic bias in which one skeletal element is lost relative to others, either by sorting or differential breakage. However, our result is independent of the counting method used to define abundance. We recalculated abundances of each isotaphonomic group as the maximum number of individuals (Gilinsky and Bennington, 1994; in this case the sum of the number of pygidia and cranidia), which should generate a negative correlation between abundance and C/P if there is a significant sorting effect. However, this also failed to produce a significant correlation with rank order of C/P (Table 3). In other words, sorting bias is not a controlling factor because abundance does not covary with sclerite sorting ratios. Instead, sorting has simply reshuffled sclerite ratios within isotaphonomic groups without significantly distorting the rank abundances of these groups.

5.2. Where have all the pygidia of micropygous taxa gone?

Hintzeturinae (Group 1) and *Politicurus* (Group 2) show extreme enrichment of cranidia in some samples (Fig. 6A, B), and this raises the question as to why there are no corresponding pygidia-rich samples. One possibility is that pygidia might be depleted by differential breakage without any corresponding bias in the abundance of cranidia. However, hintzeturine and *Politicurus* tails are thick and quite robust, and it is difficult to envisage a mechanical process that would impact only pygidia. Small cranidia would also be vulnerable, as would delicate structures of larger cranidia (e.g., various spines; posterolateral projection). However, the silicified samples from the Red Canyon Member

are characterized by exquisite preservation, without evidence for pervasive breakage (Fig. 8; see also Adrain et al., 2003, Figs. 7, 8, 12). This suggests that differential breakage is not a significant factor in our collections. Instead, we argue that the absence of pygidia-rich assemblages expected from differential sorting is likely due to collecting bias. As noted above, horizons with silicified trilobites were discovered by searching for sclerites weathering out in relief on bedding and other surfaces. The small pygidia of micropygous trilobites do not present on weathered surfaces in the same way as the larger, more conspicuous cranidia (Fig. 2C, D), and are difficult to observe in the field. Hence, pygidia-rich assemblages could easily pass unnoticed.

6. Patterns at the biofacies level

6.1. Multivariate analysis of abundance data

Multivariate analysis of trilobite abundance and/or occurrence data has a long history (e.g., Ludvigsen, 1978; Ludvigsen and Westrop, 1983; Balseiro et al., 2010; Carlucci and Westrop, 2012; Hally and Paterson, 2014), and similar techniques are used widely in paleoecological analyses (e.g., Patzkowsky and Holland, 1999; Brett et al., 2007b; Clapham and James, 2008). Moreover, widespread documentation of recurrent, environmentally related associations (biofacies; paleocommunities) of fossils (e.g., Patzkowsky and Holland, 1999; Amati and Westrop, 2006), often characterized by environmental tracking (e.g., Westrop, 1996; Brett et al., 2007a), as well as onshore-offshore gradients of species richness (e.g., Westrop and Adrain, 1998) indicate

Table 2

Correlation of rank orders of C/P ratio and $\log_{10}$ abundances (calculated with the minimum number of individuals methods; Fig. 7) for each of four isotaphonomic groups using Spearman's rho. In all cases, there is no significant correlation.

	Spearman's rho	p
Group 1	0.234	0.18
Group 2	0.115	0.71
Group 3	−0.118	0.65
Group 4	0.005	0.98

Table 3

Correlation of rank orders of C/P ratio and $\log_{10}$ abundances (calculated with the maximum number of individuals methods; not plotted as a figure) for each of four isotaphonomic groups using Spearman's rho. In all cases, there is no significant correlation.

	Spearman's rho	p
Group 1	0.192	0.28
Group 2	0.047	0.88
Group 3	−0.189	0.47
Group 4	0.067	0.72

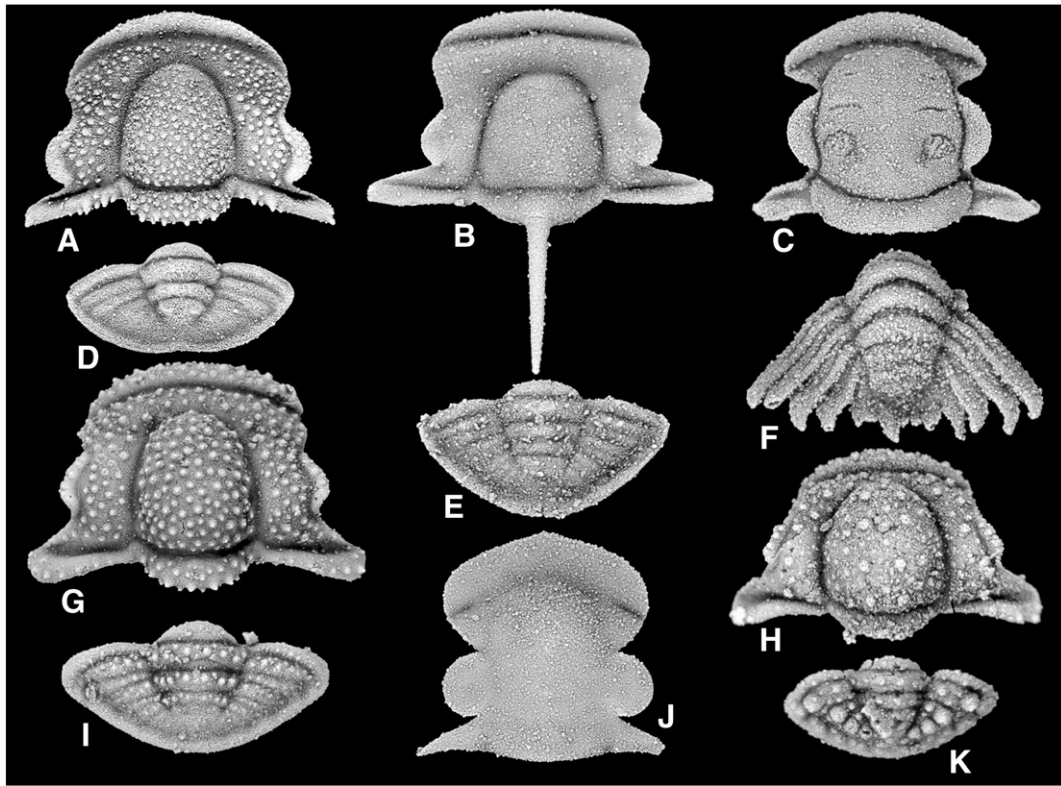


Fig. 8. Representative trilobite sclerites from the Red Canyon Member at section LDN demonstrating the quality of preservation. **A, D**, cranidium and pygidium of *Hintzecurus paragenalatus* (Ross, 1951); **B, E**, cranidium and pygidium of *Politicurus* n. sp.; **C, F**, cranidium and pygidium of *Praepatokephalus armatus* (Hintze, 1953); **G, I**, cranidium and pygidium of *Rossicurus* n. sp.; **J**, cranidium of *Xenostegium franklinense* Ross, 1951; **H, K**, cranidium and pygidium of dimeropygid n. gen. n. sp.

that ecologically significant data can be retrieved from the fossil record at the community level.

In this study, we use both classification (cluster analysis) and ordination (non-metric multidimensional scaling [NMS]) methods to define biofacies. We also test for a relationship between positions of samples along an NMS axis and the overall C/P ratio for each sample, thereby assessing the potential influence of sorting bias on biofacies groupings.

6.2. Cluster analysis

We performed cluster analysis on log-transformed genus abundance data for 34 samples using Ward's method (Fig. 9A), which is based on euclidean distances and is a space-conserving method of linkage that minimizes chaining (McCune and Grace, 2002); we obtained the same results using average linkage (unweighted pair group method with arithmetic mean) and Bray-Curtis similarity (not shown). Fig. 9A shows the samples in Q-mode clustering order along with the abundances of the dominant genera, which are also identified by the isotaphonomic group to which they belong. Two large clusters of stratigraphically segregated samples are interpreted as recording two distinct biofacies, the *Ibexicurus*-*Symphysurina* (*I-S*) and *Politicurus*-*Hintzecurus* (*P-H*) biofacies. Median values of the overall C/P ratio are not significantly different for samples assigned to each biofacies (Fig. 9B), so that the results of the cluster analysis are not influenced by sorting bias.

The biofacies are in part gradational (e.g., species of *Bellefontia* appear in the upper part of the stratigraphic range of the *I-S* Biofacies and remains abundant in the *P-H* biofacies). However, the *P-H* Biofacies also differs from the *I-S* Biofacies in the loss of species of some key taxa (*Ibexicurus*; *Symphysurina* becomes rare), and the addition of others (*Politicurus* and *Ibexicurus*). This pattern of replacement cannot be a

result of taphonomic processes, particularly the substitution of species of *Hintzecurus* for species of *Ibexicurus*, as they belong to the same isotaphonomic group. Biofacies replacement is expressed stratigraphically and, in the context of a single stratigraphic section, it is difficult to know whether this is evolutionary (addition of species, or pruning of clades by extinction) or ecological (habitat tracking with the appearance of shallow water species in the latter part of the HST). However, as similar stratigraphic changes can be seen in the succession of the Bear River Range of southern Idaho (Adrain et al., 2003; unpublished), we suspect that the changes up-section at LDN record predominantly evolutionary patterns.

6.3. Ordination

Non-metric multidimensional scaling is used widely in ecological and paleoecological analysis (see McCune and Grace, 2002, p. 125 for a summary of the advantages of this method). It was performed on the same data set as the cluster analysis and, as in the latter, euclidean distance was used as dissimilarity index. A 2-D solution was used in the Q-mode NMS because addition of a third dimension led to only a small reduction in stress values (from 0.106 to 0.07) without appreciably changing the results. Groupings of samples produced by the cluster analysis (Fig. 8) are readily recognizable in the plot of NMS axes 1 and 2 (Fig. 10A).

The positioning of samples along a gradient immediately lends itself to a test of the impact of taphonomic bias on biofacies recognition. Sample position and C/P ratio should co-vary if sorting is biasing the outcome of biofacies analysis. Fig. 10B shows a plot of C/P against scores on NMS axis 1. Rank order of C/P is not correlated with rank order of NMS scores (for axis 1 and C/P, Pearson's rho = 0.009; p = 0.96; also

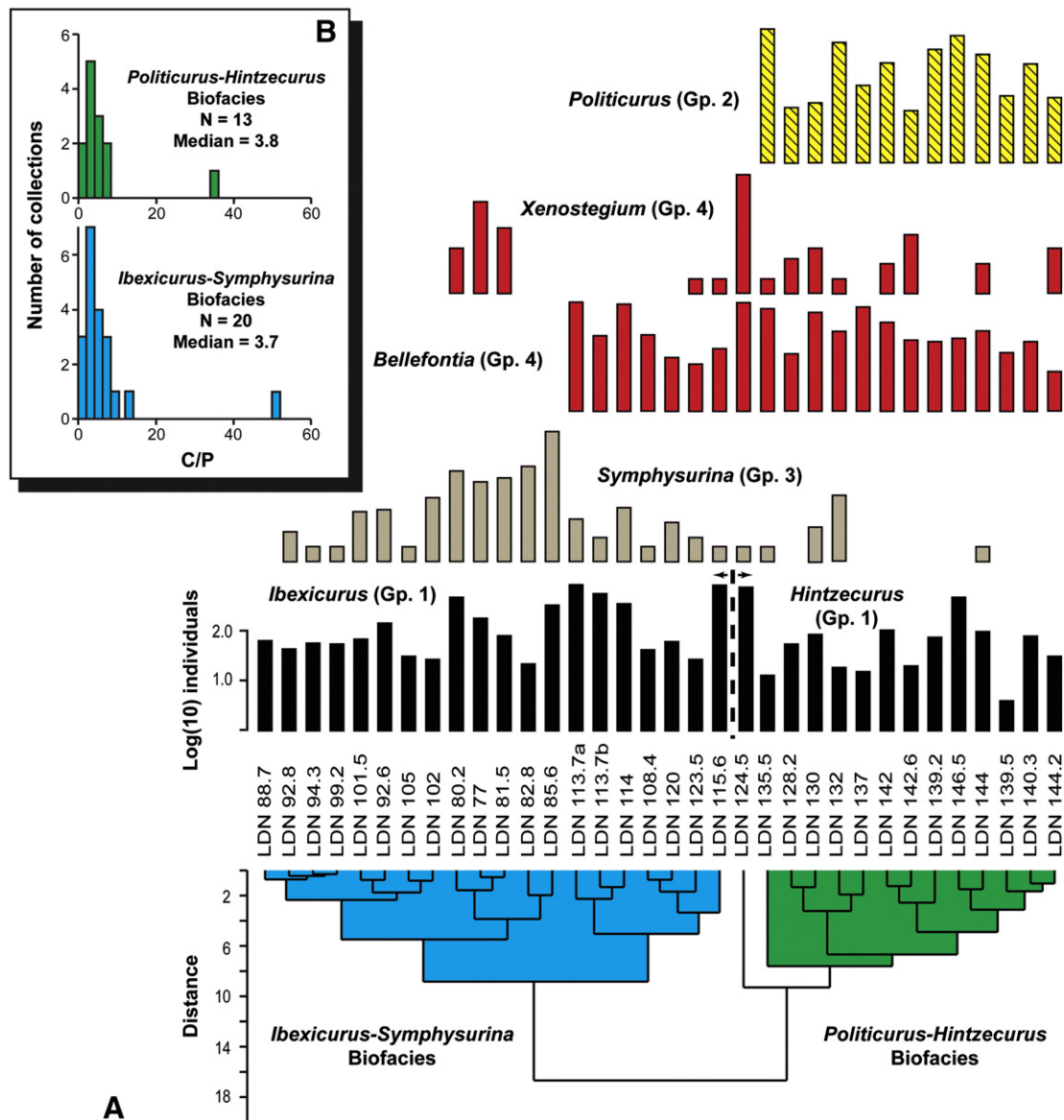


Fig. 9. A. Q-mode cluster analysis (using Ward's Method) of log transformed genus abundance data for 34 collections from the Red Canyon Member. Bar charts show the abundances of each isotaphonomic group, with groups 1 and 4 broken down into constituent genera; the dashed line separates *Ibexicurus* and *Hintzecurus* within Group 1. Two distinct biofacies are segregated stratigraphically, with the *Ibexicurus-Symphysurina* Biofacies occurring in early highstand facies, and the *Politicus-Hintzecurus* Biofacies in the later highstand succession. Collection LDN 124.5 lacks *Politicus* but includes other elements of the *Politicus-Hintzecurus* Biofacies. It is unique in having high abundance of *Parabellafontia*, and was left unassigned. **B.** Histograms of crania:pygidia (C/P) values for samples assigned to each biofacies. Median values are not significantly different (Mann-Whitney *U* test, $u = 123.5$; $p = 0.82$).

the correlation between axis 2 and C/P [not shown] was not significant), indicating that taphonomic sorting does not influence the distribution of collections along the gradient.

6.4. Species richness

To test for a potential control on species richness by taphonomic sorting, we examined the relationship between the number of species in a sample and the C/P ratio. For raw counts of species (Fig. 11A), rank orders of richness and C/P ratio are not correlated (Spearman's $\rho = -0.073$; $p = 0.60$). As sample size influences species richness, we also used rarefaction in a second analysis (Fig. 10B). We calculated the expected number of species at a standard sample size ($E[S_n]$) of 80 individuals, which represented a compromise between maintaining the highest possible sample size while retaining as many samples as possible in the analysis (with a cut-off at 80 individuals, the number of samples was reduced from 34 to 26). The net result was to shift

two samples with extreme values of C/P and low rarefied richness to the left edge of the distribution (Fig. 11B), resulting a negative correlation between rank order of C/P and $E[S_n]$, albeit one that is not significant (Spearman's ρ , -0.209 ; $p = 0.13$). This disappears when the two outliers are removed.

Samples from the *Politicus-Hintzecurus* Biofacies tend to have higher richness than those from the *Ibexicurus-Symphysurina* Biofacies, and this difference is significant with both a Mann-Whitney *U* test and a Kolmogorov-Smirnov test (Table 4); following rarefaction, the difference is significant only with a Kolmogorov-Smirnov test (Table 4).

7. Discussion

Although there was unambiguous evidence for taphonomic sorting of sclerites, we were unable to find any significant correlation between rank orders of C/P ratios and abundances, both at the level of individual isotaphonomic groups and for entire samples at the biofacies level; the

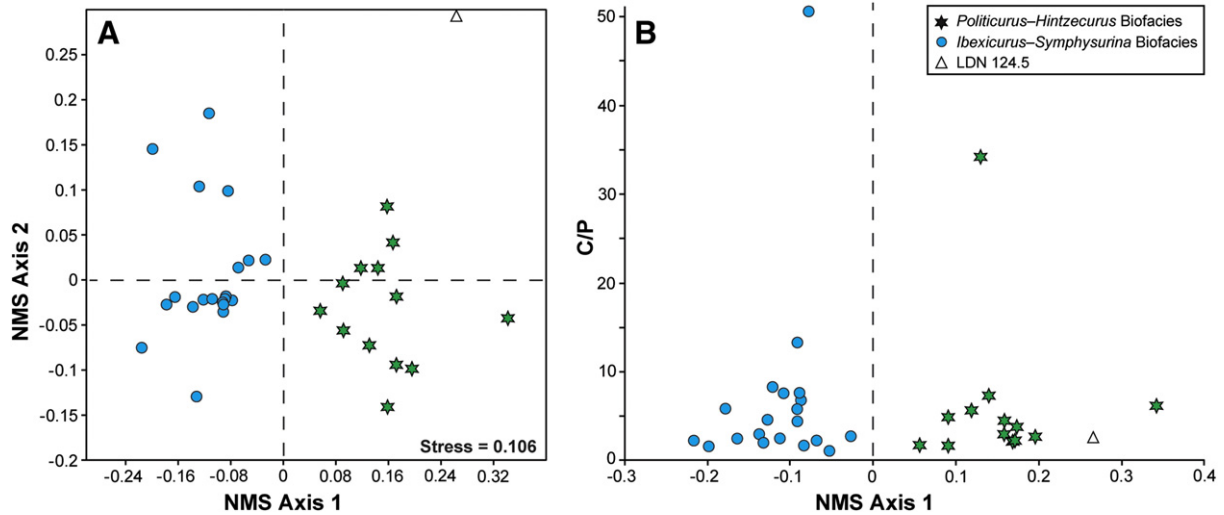


Fig. 10. A. Ordination using non-metric multidimensional scaling (NMS), using euclidean distance as a dissimilarity index; 2-D solution with stress = 0.106. Note that the groupings identified in the cluster analysis are differentiated clearly in the ordination. **B.** Plot of scores on NMS axis 1 against cranidia:pygidia (C/P) ratio for each collection. Rank orders of scores and C/P are not correlated (Spearman's rho = 0.009; $p = 0.96$).

C/P ratio of samples showed no relationship with scores along ordination axes or with the groupings produced by cluster analysis. Multivariate analysis of abundance data in this case has produced groupings of collections that have ecological significance. This must be at least in part due to the fact that each biofacies includes unique taxa, and this type of faunal replacement along an environmental gradient will be resistant to distortion by taphonomic processes (see also Westrop, 1986).

Preservational quality indicates that sorting was not accompanied by pervasive destruction of sclerites by physical breakage, suggesting relatively low energy levels during accumulation and/or, short residence times in the taphonomically active zone (TAZ; Davies et al., 1989). The absence of any stratigraphic trend in the C/P ratio indicates that there was no major change in sorting regime with upward shallowing along what was likely a modest depth gradient. Small-scale, thin, patchy accumulations of skeletal material (Fig. 2C, D) suggest that sorting involved shuffling of sclerites and that there was no large-scale lateral transport of skeletal material. It is likely that the trilobite accumulations of the Red Canyon Member have been lightly overprinted by taphonomic processes.

Our results are encouraging but our data are limited to a segment of a bathymetric gradient that lies between fairweather and mean storm wave base. At some point, we expect that taphonomic bias will start to overwhelm the ecological signal in the data, as energy level of the depositing medium increases and/or as the residence time in the TAZ increases. For example, proximal settings near fairweather wave base should be characterized by more frequent and intense reworking, and this will increase the role of differential breakage, enhance sorting, and probably lead to condensation. When most sclerite types are undergoing transportation and/or breakage, patterns of abundance and probably also species richness will become distorted. Loss of majority of sclerites of a particular isotaphonomic group will clearly be a problem. In the context of faunas similar to those documented in this study, we predict that high levels of differential breakage and sorting would lead to over-representation of large, robust tails of groups 3 and 4.

Conversely, in deeper sites near maximum storm wave base, a shift from winnowing to mud blanketing as a dominant process (e.g., Miller et al., 1988) may lead to very high ecological fidelity (e.g., Taylor and Brett, 1996), to the extent that even snapshots of behavior are preserved

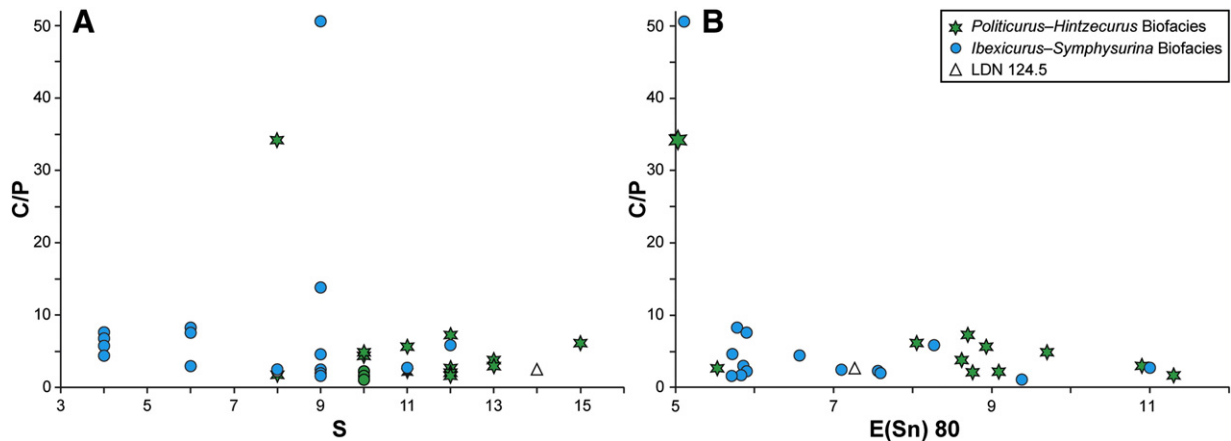


Fig. 11. A. Plot of cranidia:pygidia (C/P) ratios against species richness (S) for each collection; rank orders are not correlated (Spearman's rho, -0.073 ; $p = 0.60$; removal of the two outliers increases the value of rho to 0.021 , $p = 0.88$). **B.** Plot of C/P against rarefied species richness (expect number of species, $E[Sn]$, at a sample size of 80 individuals); rank orders are not correlated (Spearman's rho, -0.209 ; $p = 0.13$; removal of the two outliers increases the value of rho to -0.080 , $p = 0.57$). Species richness differs significantly between biofacies using both Mann-Whitney U and Kolmogorov-Smirnov tests, but is limited to the Kolmogorov-Smirnov test for a comparison of rarefied richness (Table 4).

Table 4

Comparison of frequency-distributions of raw species richness (S) and expected species richness at standard sample size of 80 individuals [E(Sn)] for the *Ibexicurus-Symphysurina* and *Politricurus-Hintzicurus* (P-H) biofacies. Test statistics are shown in regular face, p values in bold.

	M-W U-test	K-S test
S	22.5; 0.002	0.60; 0.009
E(Sn)	48; 0.07	0.54; 0.03

(e.g., Karim and Westrop, 2002). That is, bathymetric changes in taphonomic regimes (e.g., Brett and Baird, 1986) could well result in parallel shifts in reliability of ecological parameters derived from fossil assemblages.

8. Conclusions

We can never know the true living abundances of fossil assemblages, but routine documentation of environmentally related biofacies or paleocommunities in the literature demonstrates that ecologically significant data can be retrieved from the fossil record at the community level. Analysis of sclerite ratios allows further insight into the robustness of paleoecological data. Our results indicate that, at least in some relatively shallow, subtidal carbonate settings above storm wave base, taphonomic sorting does not control rank order of abundance or species richness. Similarly, sorting did not influence positions of samples along ordination axes or their classification by cluster analysis. Modern live-dead comparisons attempt to evaluate ecological fidelity of death assemblages in the face of time averaging, and suggest that rank order may be preserved in many cases. Our analysis is aimed at a different source of bias – taphonomic sorting – but our results are broadly congruent with the conclusions of modern, actualistic studies, and are cause for cautious optimism regarding the reliability of paleoecological data.

Acknowledgments

This research was supported by NSF grants EAR 0309092 and DEB 0716065. David Schultz assisted in sampling. Order of authorship is alphabetical. Nigel Hughes and an anonymous reviewer provided helpful comments on an earlier version of the manuscript.

References

- Adrain, J.M., Lee, D.C., Westrop, S.R., Chatterton, B.D., Landing, E., 2003. Classification of the trilobite subfamilies Hystricurinae and Hintzicurinae subfam. nov., with new genera from the Lower Ordovician (Ibexian) of Idaho and Utah. *Memoirs of the Queensland Museum* 48, 553–586.
- Adrain, J.M., McAdams, N.E., Westrop, S.R., 2009. Trilobite biostratigraphy and revised bases of the Tulean and Blackhillsian Stages of the Ibexian Series, Lower Ordovician, western United States. *Australasian Association of Paleontologists Memoir* 37, 541–610.
- Adrain, J.M., McAdams, N.E., Westrop, S.R., Karim, T.S., 2012. Systematics and affinity of the Lower Ordovician (Tulean; lower Floian) trilobite *Psalikilopsis*. *Australasian Association of Paleontologists Memoir* 42, 369–416.
- Adrain, J.M., Westrop, S.R., Karim, T.S., Landing, E., 2014. Trilobite biostratigraphy of the Stairsian Stage (upper Tremadocian) of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Paleontologists* 45, 167–214.
- Alexander, R.R., 1990. Disarticulated shells of Late Ordovician brachiopods: inferences on strength of hinge and valve architecture. *J. Paleontol.* 64, 524–532.
- Alin, S.R., Cohen, A.S., 2004. The live, the dead, and the very dead: taphonomic calibration of the recent record of paleoecological change in Lake Tanganyika, East Africa. *Paleobiology* 30, 44–81.
- Amati, L., Westrop, S.R., 2006. Sedimentary facies and trilobite biofacies along a shelf-basin transect, Viola Group, central Oklahoma. *PALAIOS* 21, 516–529.
- Balseiro, D., Waisfeld, B.G., Buatois, L.A., 2010. Unusual trilobite biofacies from the Lower Ordovician of the Argentine Cordillera Oriental: new insights into olenid palaeoecology. *Lethaia* 44, 58–75.
- Behrensmeier, A.K., Hook, R.W., Behrensmeier, A.K., 1992. Paleoenvironmental contexts and taphonomic modes. In: Damuth, J., DiMichele, W.A., Potts, R., Sues, H.-D., Wing,

- S.L. (Eds.), *Terrestrial Ecosystems Through Time*. Chicago University Press, pp. 17–136.
- Brandt, D.S., 1996. Epizoans on *Flexicalymene* (Trilobita) and implications for trilobite palaeoecology. *J. Paleontol.* 70, 442–449.
- Brett, C.E., Baird, G.C., 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *PALAIOS* 1, 207–227.
- Brett, C.E., Hendy, A.J.W., Bartholomew, A.J., Bonelli, J.R., McLaughlin, P.L., 2007a. Response of shallow marine biotas to sea level fluctuations: a review of faunal replacement and the process of habitat tracking. *Palaia* 22, 228–244.
- Brett, C.E., Bartholomew, A.J., Baird, G.C., 2007b. Biofacies recurrence in the Middle Devonian of New York State: an example with implications for evolutionary paleoecology. *PALAIOS* 22, 306–324.
- Carlucci, J.R., Westrop, S.R., 2012. Trilobite biofacies along an Ordovician (Sandbian) carbonate buildup to basin gradient, southwestern Virginia. *PALAIOS* 27, 19–34.
- Clapham, M.E., James, N.P., 2008. Paleocology of early-middle Permian marine communities in eastern Australia: response to global climate change in the aftermath of the Late Paleozoic ice age. *PALAIOS* 23, 738–750.
- Davies, D.J., Powell, E.N., Stanton, R.J., 1989. Relative rates of shell dissolution and net sediment accumulation – a commentary: can shell beds form by the gradual accumulation of biogenic debris on the sea floor? *Lethaia* 22, 207–212.
- Edinger, E.N., Pandolfi, J.M., Kelley, R.A., 2001. Community structure of Quaternary coral reefs compared with Recent life and death assemblages. *Paleobiology* 27, 669–694.
- Fortey, R.A., 1975. Early Ordovician trilobite communities. *Fossils Strata* 4, 331–352.
- Fortey, R.A., Owens, R.M., 1990. Trilobites. In: McNamara, K.J. (Ed.), *Evolutionary Trends*. Belhaven Press, London, pp. 121–142.
- Fortey, R.A., Owens, R.M., 1997. Evolutionary history. In: Whittington, H.B., et al. (Eds.), *Treatise on Invertebrate Paleontology, Part O, Revised, Trilobita*. Geological Society of America, Boulder, Colorado, and University of Kansas Press Vol. 1. Lawrence, Kansas, pp. 249–286.
- Gilinsky, N.L., Bennington, J.B., 1994. Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. *Paleobiology* 20, 245–258.
- Greenstein, B.J., 1993. Is the fossil record really so poor? A comparison of living and sub-fossil assemblages. *PALAIOS* 8, 587–601.
- Hally, L.A., Paterson, J.R., 2014. Biodiversity, biofacies and biogeography of middle Cambrian (Series 3) arthropods (Trilobita and Agnostida) on the East Gondwana margin. *Gondwana Res.* 26, 654–674.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaentol. Electron.* 4, 1–9.
- Havens, K.J., McConaughy, J.R., 1990. Molting in the mature female blue crab, *Callinectes sapidus* Rathbun. *Bull. Mar. Sci.* 46, 37–47.
- Hintze, L.F., 1953. Lower Ordovician trilobites from western Utah and eastern Nevada. *Utah Geol. Mineral. Surv. Bull.* 48, 1–249.
- Karim, T., Westrop, S.R., 2002. Taphonomy and paleoecology of Ordovician trilobite clusters, Bromide Formation, south-central Oklahoma. *PALAIOS* 17, 394–403.
- Kidwell, S.M., 2001. Preservation of species abundance in marine death assemblages. *Science* 94, 1091–1094.
- Kidwell, S.M., 2002. Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance. *Geology* 30, 803–806.
- Kidwell, S.M., 2013. Time-averaging and fidelity of modern death assemblages: building a taphonomic foundation for conservation biology. *Palaentology* 56, 87–522.
- Lockwood, R., Chasant, L.R., 2006. Quantifying taphonomic bias of compositional fidelity, species richness, and rank abundance in molluscan death assemblages from the upper Chesapeake Bay. *PALAIOS* 21, 376–383.
- Ludvigsen, R., 1978. Middle Ordovician trilobite biofacies, southern Mackenzie Mountains. *Geol. Assoc. Can. Spec. Pap.* 18, 1–33.
- Ludvigsen, R., Westrop, S.R., 1983. Trilobite biofacies of the Cambrian-Ordovician boundary interval in northern North America. *Alcheringa* 7, 301–319.
- McAdams, N., Adrain, J.M., 2011a. Systematics of the Lower Ordovician pliomeric trilobite *Hintzeia*, with species from the Great Basin, western USA. *Zootaxa* 2910, 1–45.
- McAdams, N.E.B., Adrain, J.M., 2011b. *Panispaspis*, a new genus of pliomeric trilobites from the lower Ordovician (Ibexian; Tulean and Blackhillsian) of the Great Basin, western USA. *Zootaxa* 2969, 1–68.
- McAdams, N.E.B., Adrain, J.M., 2011c. Revision of the Lower Ordovician (lower Floian; Tulean) pliomeric trilobite *Protopliomerella*, with new species from the Great Basin, western USA. *Zootaxa* 3144, 1–113.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon 300 pp.
- Miller, K.B., Brett, C.E., Parsons, K.M., 1988. The palaeoecological significance of storm-generated disturbance within a Middle Devonian muddy epicritic sea. *PALAIOS* 3, 35–52.
- Miller, J.F., Evans, K.R., Loch, J.D., Ethington, R.L., Stitt, J.H., 2001. New lithostratigraphic units in the Notch Peak and House formations (Cambrian-Ordovician), Ibex area, western Millard County, Utah. *Brigham Young University Geology Studies* 46, 35–69.
- Miller, J.F., Evans, K.R., Loch, J.D., Ethington, R.L., Stitt, J.H., Holmer, L.E., Popov, L.E., 2003. Stratigraphy of the Sauk III Interval (Cambrian-Ordovician) in the Ibex area, western Millard County, Utah and central Texas. *Brigham Young University Geology Studies* 47, 23–118.
- Moore, J.R., Norman, D.B., 2009. Quantitatively evaluating the sources of taphonomic biasing of skeletal element abundances in fossil assemblages. *PALAIOS* 24, 591–602.
- Oliszewski, T.D., Kidwell, S.M., 2007. The preservational fidelity of evenness in molluscan death assemblages. *Paleobiology* 33, 1–23.
- Patzkowsky, M.E., Holland, S.M., 1999. Biofacies replacement in a sequence stratigraphic framework: Middle and Upper Ordovician of the Nashville dome, Tennessee, USA. *PALAIOS* 14, 301–317.
- Pratt, B.R., 2010. Peritidal carbonates. In: James, N.P., Dalrymple, R.W. (Eds.), *Facies Models 4*. Geological Association of Canada Geotext Vol. 6, pp. 401–420.

- Ross Jr., R.J., Hintze, L.F., Ethington, R.L., Miller, J.F., Taylor, M.E., Repetski, J.E., 1997. The Ibexian, lowermost Series in the North American Ordovician, with a section on Echinoderm Biostratigraphy by J. Sprinkle and T.E. Guensburg. In: Taylor, M.E. (Ed.), *Early Paleozoic Biochronology of the Great Basin, Western United States*. United States Geological Survey Professional Paper Vol. 1579, pp. 1–50.
- Saltzman, M.R., Edwards, C.T., Adrain, J.M., Westrop, S.R., 2015. Persistent oceanic anoxia and elevated extinction rates separate the Cambrian and Ordovician radiations. *Geology* 43, 807–810.
- Tamone, S.L., Taggart, S.J., Andrews, A.G., Mondragon, J., Nielson, J.K., 2007. The relationship between circulating ecdysteroids and chela allometry in male Tanner crabs: evidence for a terminal molt in the Genus *Chionoecetes*. *J. Crustac. Biol.* 27, 635–642.
- Taylor, W.L., Brett, C.E., 1996. Taphonomy and paleoecology of echinoderm lagerstätten from the Silurian (Wenlockian) Rochester Shale. *PALAIOS* 11, 118–140.
- Tomašových, A., 2006. Linking taphonomy to community-level abundance: insights into compositional fidelity of the Upper Triassic shell concentrations (Eastern Alps). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 235, 355–381.
- Tomašových, A., Kidwell, S.M., 2009. Preservation of spatial and environmental gradients by death assemblages. *Paleobiology* 35, 119–145.
- Walls, E.A., Berkson, J., Smith, S.A., 2002. The horseshoe crab, *Limulus polyphemus*: 200 million years of existence, 100 years of study. *Rev. Fish. Sci.* 10, 39–73.
- Westrop, S.R., 1983. The life habits of the Ordovician illaenine trilobite *Bumastoides*. *Lethaia* 16, 15–24.
- Westrop, S.R., 1986. Taphonomic versus ecologic controls on taxonomic relative abundance patterns in tempestites. *Lethaia* 19, 123–132.
- Westrop, S.R., 1996. Temporal persistence and stability of Cambrian biofacies: Sunwaptan (Upper Cambrian) trilobite faunas of North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127, 33–46.
- Westrop, S.R., Adrain, J.M., 1998. Trilobite alpha diversity and the reorganization of Ordovician benthic marine communities. *Paleobiology* 24, 1–16.
- Zecchin, M., Catuneanu, O., 2013. High-resolution sequence stratigraphy of clastic shelves I: units and bounding surfaces. *Mar. Pet. Geol.* 39, 1–25.