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Testing for taphonomic bias in deep time using trilobite sclerite ratios

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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.

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

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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., Behrensmeyer 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),

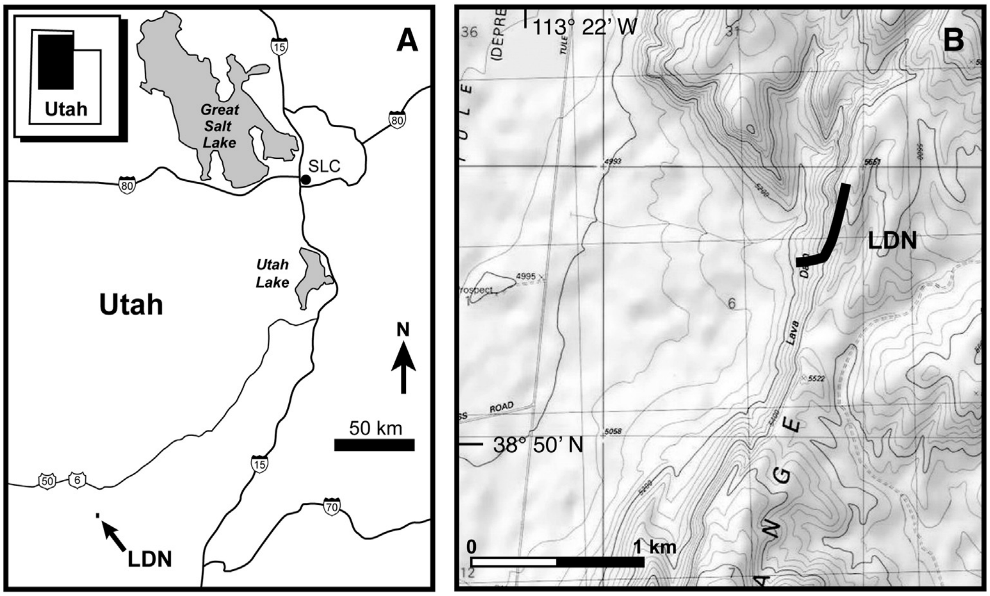

Fig. 1. Maps showing the location of section LDN (Lava Dam North).

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