



Microstratigraphy, trilobite biostratigraphy, and depositional environment of the “Lower Cambrian” Ruin Wash Lagerstätte, Pioche Formation, Nevada

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ABSTRACT

The uppermost 43 cm of Dyeran strata at the Ruin Wash Lagerstätte (Chief Range, Lincoln County, Nevada) contain nonmineralized invertebrates and exceptionally preserved, articulated olenelloid trilobites. However, the environmental factors responsible for the preservation of olenelloids in this unusual state at Ruin Wash have received little study and are therefore poorly understood. Microstratigraphic analysis of this interval reveals that the strata, comprised almost exclusively of clay-sized particles and rather monotonous and featureless in outcrop, were deposited as a series of thin event beds interpreted as tempestites. The energy of deposition progressively waned then waxed through the interval, and benthic redox conditions shifted concurrently. Biostratigraphic data for more than 500 trilobite specimens encountered in the measured section reveal that the trilobite fauna was autochthonous, although winnowed surfaces rich in bioclasts occurring at the base and top of the section indicate intervals of prolonged pre-burial exposure time and/or *in situ* reworking. Trilobite biostratigraphy was strongly influenced by subtle environmental shifts: the degree of disarticulation and sclerite fracturing correlate positively with event bed energy and inferred bottom-water oxygen content. These results demonstrate that (1) preservation of articulated trilobites is favoured near the distal limit of scouring associated with depositional events, where rapid sedimentation occurs in the absence of substrate reworking; and (2) differential taphonomic overprint on trilobite preservation can occur within a monofacial succession, driven by subtle environmental change insufficient to leave a distinct lithological signature. This highlights the need for careful microstratigraphic, sedimentological, and ichnological analysis prior to comparison of palaeobiological or palaeoecological parameters inferred from fossil assemblages, even when the assemblages occur within the same lithofacies.

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1. Introduction

Strata of the uppermost 43 cm of the Combined Metals Member (Pioche Formation, uppermost Dyeran Stage, Cambrian) at the Ruin Wash locality, Chief Range, Lincoln County, Nevada (Fig. 1) contain a diverse fauna of excellently preserved olenelloid trilobites (Palmer, 1998a; Fig. 2) and other invertebrates (Lieberman, 2003). This short stratigraphic interval qualifies as both a concentration Lagerstätte (on account of the abundance of trilobite remains) and a conservation Lagerstätte (on account of the preservation of nonmineralized organisms and of olenelloid trilobites in an unusual, articulated state). In March 1999, a multi-institutional consortium involving the University of California, Riverside (UCR), the Museum of Comparative Zoology at Harvard University (MCZ), and the Peabody Museum at Yale University (YPM) in collaboration with the Bureau of Land Management (BLM) conducted an extensive excavation of the site in

order to carefully document the occurrence of the fossil biota and to recover a large number of specimens for research. Articulated trilobites can provide a wealth of palaeobiological and palaeoecological information, and the material collected during this and earlier excavations at Ruin Wash has already provided insight into issues of taphonomy (Webster and Hughes, 1999), systematics and phylogeny (Webster et al., 2001; Paterson and Edgecombe, 2006), and palaeobiology (Palmer, 1998a; Webster et al., 2001; Webster and Zelditch, 2005; Webster, 2007a). However, the depositional setting of the Lagerstätte, and consequently the environmental controls responsible for the exquisite fossil preservation, has received little attention.

The present paper documents the microstratigraphy, sedimentology, ichnology, and trilobite biostratigraphy of the Ruin Wash Lagerstätte, which together permit detailed inference of the depositional environment in which this unit accumulated. Here, we aim to improve understanding of the relationship between depositional setting and trilobite preservation; environmental factors responsible for the preservation of the nonmineralized organisms will be discussed elsewhere. Our integrative study demonstrates a strong dependence of

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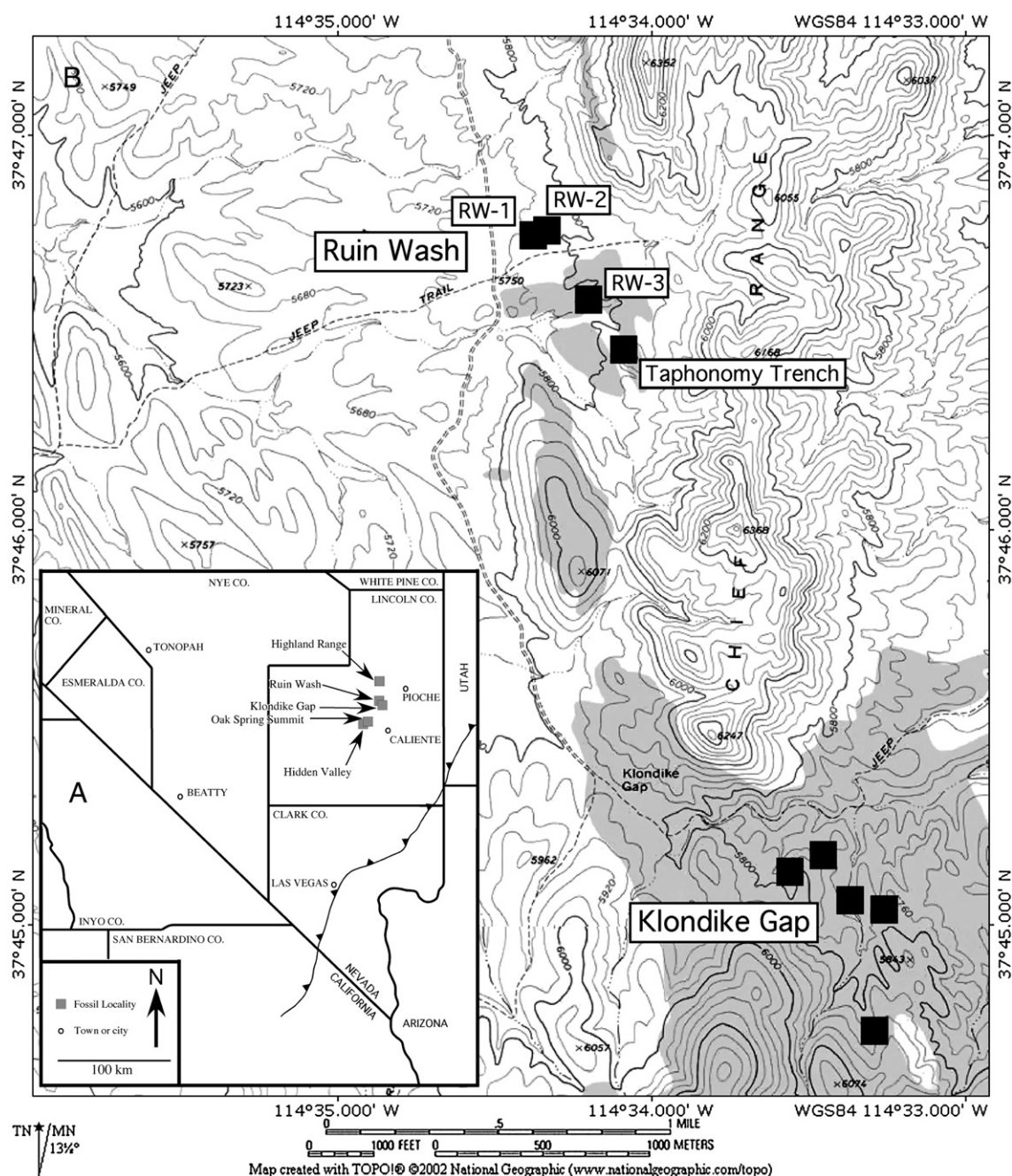


Fig. 1. A, Map showing location of the Ruin Wash Lagerstätte on the western flank of the Chief Range, Lincoln County, Nevada, southwestern United States. Other localities mentioned in the text are shown (see also Palmer, 1998a). Black line with triangles mark eastern limit of thrusting of Sevier Orogenic Belt (overthrust block to west). B, Detailed map of the Ruin Wash locality showing the trenches from which the invertebrate fauna has been recovered. The detailed excavation described herein was conducted at the “taphonomy trench” (Fig. 3). Sites at Klondike Gap to the south represent the closest well-studied outcrop of correlative strata (Webster, 2007b), but yield fossils of unremarkable preservational quality. Map created with TOPO! software (© National Geographic, 2002).

trilobite preservation on subtle changes in depositional conditions within this short, monofacial section. Resolving such environmental controls over trilobite preservation is important for understanding the distribution of trilobite Lagerstätten and of complete trilobites in general, and for identifying potential taphonomic bias when comparing palaeobiological and palaeoecological parameters inferred from fossil assemblages.

2. Materials and methods

The taphonomic data presented herein stem from the “taphonomy trench” dug by MW and NCH as part of the major excavation in 1999

(Fig. 1b). The material collected is now housed in the Geology Museum at UCR, the MCZ, the YPM, the Field Museum of Natural History, Chicago (FMNH), and the Institute for Cambrian Studies, Department of the Geophysical Sciences, University of Chicago (ICS).

The “taphonomy trench” refers to a pit systematically excavated for the specific purpose of collecting biostratigraphic data during the 1999 operation. The pit exposed a rock surface approximately 2 m by 2 m in area (Fig. 3). The stratigraphically highest bed within the trench was the ribbon limestone marking the base of the Comet Shale Member (basal Delamaran Stage; Palmer, 1998b; Sundberg and McCollum, 2000), which immediately overlies the Ruin Wash Lagerstätte (Fig. 4). Over the course of a week, the trench was deepened by progressively

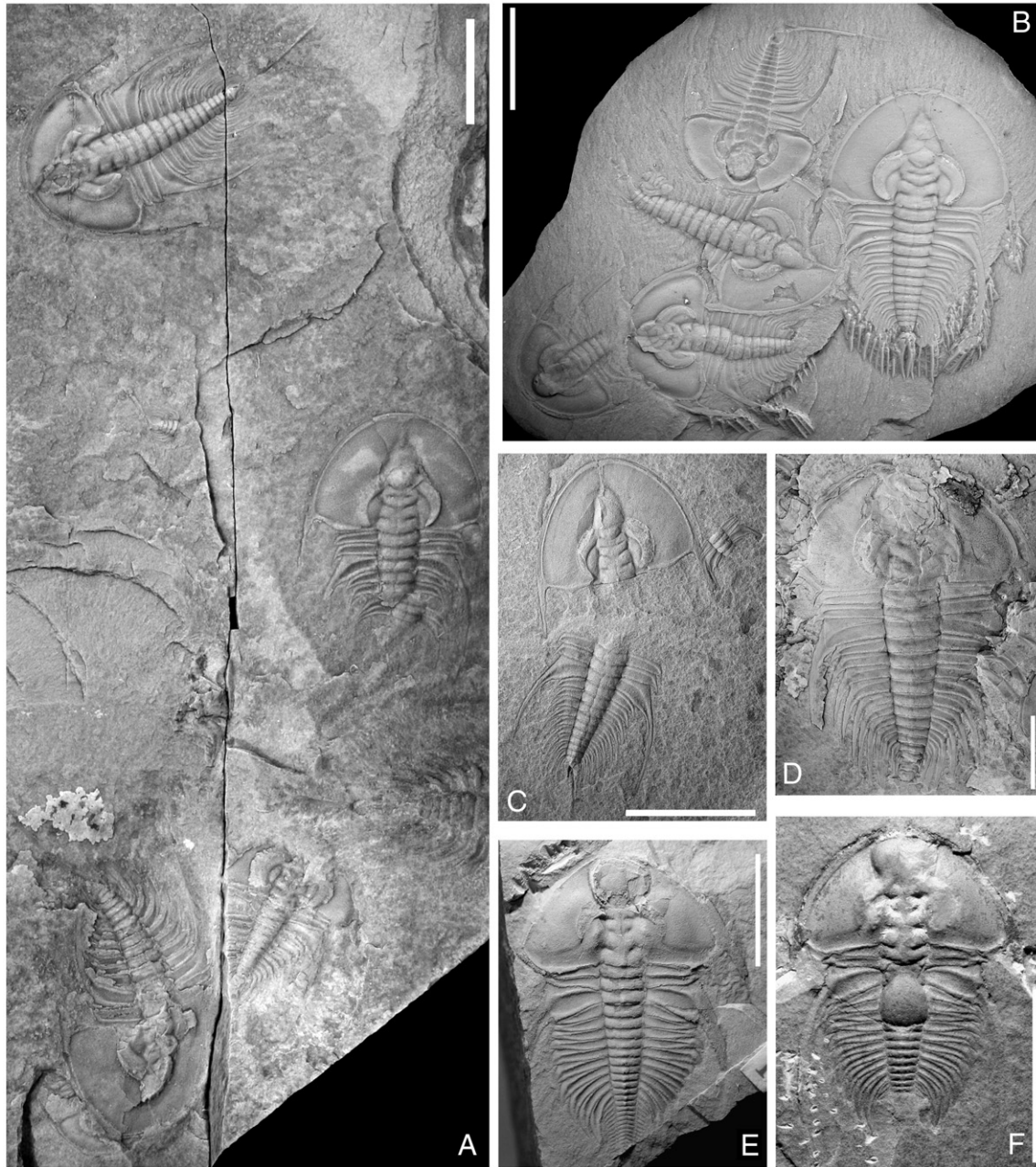


Fig. 2. Exceptionally preserved olenelloid trilobites from the Ruin Wash Lagerstätte. A, B, Clusters of large, articulated cephalothoraces of *Olenellus gilberti* and *Olenellus chiefensis*. Specimens on each slab show a hint of preferred orientations in two orthogonal directions (roughly top/bottom and left/right as illustrated). Several of the specimens retain a hypostome in life position, and are interpreted as minimally disturbed carcasses. A, Internal moulds; ICS-1044.50. B, Latex cast of ICS-1044.10. C, Slightly disarticulated dorsal exoskeleton of *O. chiefensis*; internal mould; UCR 9945.70. D, Complete dorsal exoskeleton of *O. gilberti*, including opisthothorax and pygidium; internal mould; UCR 9945.43. E, Minimally disrupted articulated exoskeleton of *Nephrolenellus geniculatus* with hypostome retained in life position, interpreted as a carcass; internal mould; FMNH PE57943. F, Minimally disrupted articulated exoskeleton of *N. geniculatus* with hypostome and rostral plate rotated 180° ventrally (pivoting at the base of the genal spines) relative to life position and now visible upside-down and pointing posteriorly down the thorax on this internal mould, interpreted as an exuvium; UCR 9945.126. Scale bars = 10 mm.

stripping off the top layers, centimetre by centimetre, thus exposing progressively older strata in the uppermost Combined Metals Member. The ribbon limestone underlying the Lagerstätte beds, 43 cm below the base of the Delamarian, marked the lower limit of the excavation (Fig. 4); the top of this limestone marks the zero datum in the measured section. Taphonomic attributes (Table 1) were recorded for more than 500 trilobite fossils encountered during this microstratigraphic sampling. A similar methodology of exhaustive microstratigraphic sampling has been employed by Schumacher and Shrake (1997), Hughes and Cooper (1999), Brett et al. (2006), and Hunda et al. (2006) in their studies of Upper Ordovician deposits from Ohio and Ontario; high-resolution sampling has also been utilized in

taphonomic and palaeoecological studies of Cambrian strata (e.g., Hughes, 1993; Gaines and Droser, 2003; Paterson et al., 2007). The six olenelloid species commonly occurring at Ruin Wash (*Olenellus gilberti*, *Olenellus chiefensis*, *Olenellus terminatus*, *Olenellus fowleri*, *Nephrolenellus geniculatus*, and *Bolbolenellus brevispinus*) a rare new species of *Zacanthopsis*, and a very rare oryctocephalid were recovered from the “taphonomy trench”. The three rarest species known to occur in the Ruin Wash Lagerstätte [a simple ptychoparioid, *Olenellus howelli*, and a new species of *Olenellus* (= “*Olenellus (Paedeumias)* sp.” of Palmer, 1998a)] were not found during the excavation. Descriptions of the two new species, based on newly collected material from several additional localities, will appear elsewhere. Soft-tissue



Fig. 3. Field photograph of the “taphonomy trench”, from which the trilobite biostratigraphic data presented herein were collected. Ruler and notebook for scale. See Fig. 1 for locality map, and text for details.

preservation was encountered in the “taphonomy trench” in the form of finely comminuted algal(?) material (see below) but remains of nonmineralized invertebrates (Lieberman, 2003) were not, likely due to their general rarity and their relatively low visibility on freshly exposed (as opposed to weathered) surfaces.

Nine successive units (labeled Unit A through I, from oldest to youngest; Fig. 4) were identified in the field based on prominent marker horizons and natural rock breakage within the “taphonomy trench”. Subsequent microstratigraphic analyses revealed that, although typically bounded by prominent hash surfaces (see below) or ichnological features (Fig. 4), successive units do not represent discrete beds nor are they considered to represent genetically distinct depositional regimes (see Inferred Depositional Environment section, below). For convenience of description, however, trilobite biostratigraphic data are binned with reference to these units.

To assess the abundance of bioclasts at particular horizons, a 15 cm by 15 cm quadrat was randomly placed on the rock surface parallel to bedding, and the taphonomic attributes of all sclerites found within the quadrat were recorded.

Subsequent to the 1999 excavation, a complete section through the 43 cm interval was extracted for laboratory examination by RRG. The section was slabbed perpendicular to bedding and X-radiographed, then logged at the millimetre scale using polished blocks and X-radiographs. The resulting data were augmented through scanning electron microscopy (SEM) and thin-section analyses of selected samples. These studies provided detailed microstratigraphic, sedimentological, and ichnological data which complemented the trilobite biostratigraphic data from the “taphonomy trench”, resulting in the integrative analysis of depositional conditions presented here.

The Ruin Wash Lagerstätte is assigned to the uppermost Dyeran Stage, Waucoban Series of the traditional Laurentian “Lower Cambrian” (Palmer, 1998b); this will likely fall within provisional Stage 4, Series 2 of the developing global standard chronostratigraphic scale for the Cambrian System (Zhu et al., 2006). The strata bearing the

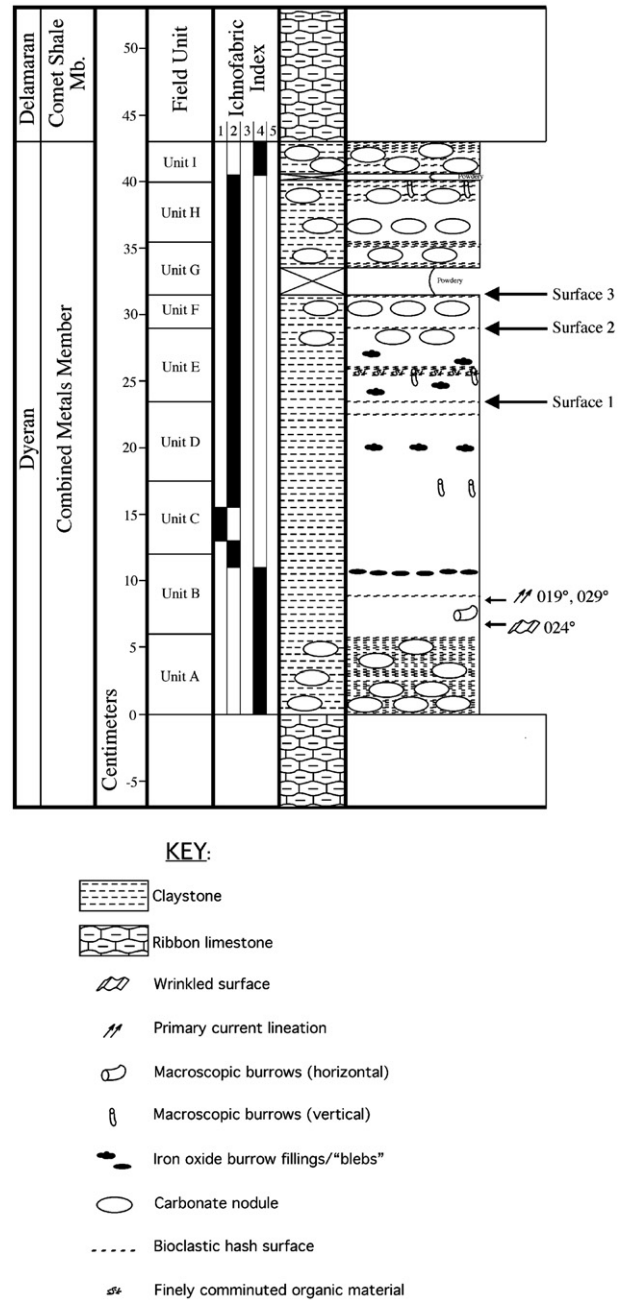


Fig. 4. Detailed log of the Ruin Wash Lagerstätte. Field units represent arbitrary subdivisions of the succession identified in the field based on prominent marker horizons and natural rock breakage within the “taphonomy trench”. Field unit A (0 cm to 6 cm above base of section) was characterized by the presence of abundant amalgamating hash surfaces and carbonate nodules; the top of field unit B (12 cm above base of section) was defined by a prominent breakage plane just above a horizon of iron oxide “blebs”; the top of field unit C (17.5 cm above base of section) was defined by a horizon penetrated by several macroscopic, vertical, iron-filled burrows; field units D, E, F, and G were separated from each other by prominent bioclastic hash surfaces [Surfaces 1 (23.5 cm above base of section), 2 (29 cm above base of section), and 3 (31.5 cm above base of section), respectively]; field unit G (31.5 cm to 35.5 cm) was capped by a series of relatively thick hash surfaces; and field units H and I were separated by a prominent hash surface penetrated by several macroscopic, vertical burrows (40 cm above base of section). The log illustrated here was taken from the “taphonomy trench”, but is typical of measured sections taken in other trenches at Ruin Wash (Fig. 1b). See text for details.

Table 1

Taphonomic attributes recorded for each trilobite fossil encountered during the systematic excavation of the “taphonomy trench”

Attribute	States
Horizon of occurrence	In centimetres, measured from the top of the ribbon limestone at the base of the section
Species identification	<i>Olenellus gilberti</i> <i>Olenellus fowleri</i> <i>Olenellus chiefensis</i> <i>Olenellus terminatus</i> <i>Nephrolenellus geniculatus</i> <i>Bolbolenellus brevispinus</i> <i>Olenellus</i> sp. indet. <i>Zacanthopsis</i> sp. Unidentifiable
Bioclast type	Cephalothorax Articulated thoracic segments Isolated cephalon Isolated hypostome Isolated thoracic segment
Bioclast orientation	Azimuth direction, relative to present-day north
Bioclast attitude	Life attitude (dorsal-up) Inverted (dorsal-down)
Bioclast fragmentation	Complete Fragmentary (including description of fracture location)
Bioclast size	In millimetres

Orientation and size were taken along the sagittal axis of cephalo/hypostomes, and the transverse axis of isolated thoracic segments. For fragmentary sclerites or sclerites with long, spinose extensions, the length and orientation along the maximal dimension was also recorded (since the response of such bioclasts during current-alignment or size-sorting is unknown). For articulated thoracic segments (with or without associated cephalo), the number of segments in a run was recorded. The precise nature of fragmentation of fragmentary cephalo and thoracic segments was also documented, but those data were not analyzed in the present study.

exceptionally preserved trilobite fauna were originally assigned to the informal “C-Shale member” of the Pioche Formation (Merriam, 1964; Palmer, 1998a), but recent revision and formalization of the lithostratigraphic nomenclature (Sundberg and McCollum, 2000; followed here) places the unit within the uppermost Combined Metals Member. Contrary to Lieberman (2003), all *Olenellus*-bearing strata within the Pioche Formation are assigned to the Combined Metals Member or the underlying Delamar Member: the Comet Shale Member is entirely Delamaran in age (Sundberg and McCollum, 2000).

3. Regional depositional setting

The uppermost Combined Metals Member was deposited on a broad shelf sea covering what is now the southern Great Basin (Palmer and Halley, 1979; Palmer, 1998a; Sundberg and McCollum, 2000). Unlike during other Cambrian intervals, a major carbonate belt appears not to have been developed in this region across the Dyeran–Delamaran (traditional “Lower–Middle Cambrian”) stage boundary (although carbonate accumulation did locally persist across the boundary in the northern Highland Range; Fig. 1; Palmer, 1998a; Sundberg and McCollum, 2000), and characterization of this portion of the Pioche Formation as lying on the “seaward margin of the carbonate platform” (Lieberman, 2003) is probably incorrect. Accumulation of the Mule Spring Limestone of western Nevada and eastern California, which represents an upper Dyeran carbonate belt outboard of the Pioche Formation, terminated just prior to deposition of the uppermost Combined Metals Member in east-central Nevada (McCollum and McCollum, 1994; McCollum and Sundberg, 1999; Sundberg and McCollum, 2003). Only coarse siliciclastics are known from correlative localities shoreward (to the present-day northeast) of the Combined Metals Member (e.g., Robison and Hintze, 1972). In the absence of a geographically intervening carbonate belt facies, the inner and outer detrital belt facies cannot be delimited and the traditional tripartite model

of shelf lithofacies (Palmer and Halley, 1979) is inapplicable to this portion of Laurentia for uppermost Dyeran to basal Delamaran deposits. Absence of the major carbonate belt “barrier” from the shelf (apparently terminated by drowning; see below) may explain the occurrence of typical “outer shelf” trilobites such as *Bathynotus* and oryctocephalids in the uppermost Combined Metals Member (Sundberg and McCollum, 1997; Palmer, 1998a), which was deposited well inboard of the shelf edge.

Sequence stratigraphic data indicate that termination of the shallow water Mule Spring Limestone and its lateral equivalents (the Chambless Limestone, the Gold Ace Limestone Member of the Carrara Formation, and the cliff-forming lower portion of the Combined Metals Member of the Pioche Formation) was associated with a rise in relative sea level (McCollum and McCollum, 1994). The overlying, predominantly siliciclastic, units (the Emigrant Formation, the Cadiz Formation, the basal Pyramid Shale Member of the Carrara Formation, and the upper portion of the Combined Metals Member south of the northern Highland Range) represent transgressive and highstand systems tract packages. Some southern Great Basin sections record a shallowing event at or near to the base of the Delamaran with a subsequent deepening in the earliest Delamaran (McCollum and McCollum, 1994). Evidence for this Dyeran–Delamaran shallowing event is scant in the Pioche Formation (Palmer, 1998a), and more regional work is necessary to determine whether the contact between the uppermost Combined Metals Member (Dyeran) and the ribbon limestone representing the base of the Comet Shale Member (Delamaran) represents a cryptic unconformity (McCollum and McCollum, 1994). However, none of the newly refined, high-resolution trilobite zones (Webster, 2003) are missing and the temporal magnitude of any such unconformity would be small.

Estimates of the accumulation time for the entire 43 cm interval studied here range from the scale of decades to a few thousand years, based on an unpublished compilation of shelf-slope depositional rates made available by P. M. Sadler. This is in close agreement with biostratigraphic data (see below) which suggest accumulation over a total of tens of thousands of years, most of which is incorporated within time-rich hash surfaces.

4. Geographic extent of the Lagerstätte

In uppermost Dyeran strata, the preservation of exceptionally preserved, articulated trilobites and nonmineralized invertebrates does not extend beyond the Ruin Wash locality. Correlative strata at adjacent localities to the north (Highland Range; Fig. 1a) and to the south (e.g., Klondike Gap, Oak Spring Summit, Hidden Valley; Fig. 1a, b) of Ruin Wash contain the same olenelloid trilobite fauna but preserved in unremarkable condition and in a disarticulated state (Webster, 2007b; unpublished data). Nonmineralized invertebrates occur in the basal Delamaran Comet Shale Member in the Highland Range (Lieberman, 2003), and are therefore younger than the fauna of the Ruin Wash Lagerstätte.

5. Microstratigraphic details of the Lagerstätte

A more detailed knowledge of the depositional setting of the Ruin Wash Lagerstätte can be gleaned through microstratigraphic study of the lithology, sedimentary structures, bed architecture, bioturbation, and distribution of iron oxides (formerly pyrite; see below) through the section (Fig. 4). Such data were gathered during systematic excavation of the “taphonomy trench” and subsequent laboratory analysis of samples, and are presented in the following paragraphs. These data are interpreted in the Inferred Depositional Environment section, below.

5.1. Lithology, sedimentary structures and bed architecture

Except for the development of several bioclast-rich hash surfaces and units rich in carbonate nodules (see below), the Ruin Wash mudstone succession appears featureless and largely monotonous in outcrop. However, analysis of polished slabs, thin sections and X-

radiographs reveals that the succession consists of numerous discrete clay beds (Fig. 5a). Each of the nine units within the Ruin Wash succession recognized in the field (Fig. 4) consists of multiple amalgamated clay beds.

The interval examined is comprised entirely of claystone with only minor silt present. A silt-sized fraction was only detected in the basal 12 cm and upper 2.5 cm of the section; the grains are most commonly associated with trilobite hash layers and occur rarely as dispersed grains within the clay matrix and as lenses or thin beds less than 1 mm in thickness. The interval from 12 cm to 40.5 cm above the base of the section consists entirely of clay-sized particles. Individual depositional beds range from 1 mm to 20 mm in thickness (average 4.7 mm), and are recognized in polished slab on the basis of colour gradation. Beds exhibit tan bases, which are commonly floored by trilobite sclerites, and grade upwards into grey tops (Fig. 5a). This gradational trend is also apparent in X-radiograph (Fig. 5b), where bed bases appear darker than bed tops, indicating that bed tops are more opaque to X-rays. SEM analyses revealed no systematic mineralogical or grain size or grain orientation trends across individual beds, and that claystones from all parts of the interval are characterized by random clay microfabrics (Fig. 6a).

Carbonate nodules are dispersed throughout the basal 6 cm and from 28 cm to the top of the section, but are absent in between (Fig. 4). Nodule size is non-uniform: those developed at the top of field units E, G, and I ranged from several millimetres to 6 cm, 4 cm, and 3 cm in diameter, respectively, whereas the maximal size of nodules close to the top of field unit H was much smaller. At least in field unit I, single nodules include several primary bedding surfaces, suggesting that the nodules grew within the host sediment during early diagenesis prior to substantial sediment compaction. Silicified and phosphatic fossils within the nodules (see below) are not compacted, confirming that the carbonates were more resistant to volume loss during burial diagenesis than the surrounding mud. Velechovsky (1985) also noted that isolated carbonate nodules within the Combined Metals Member grew *in situ*, based on observations of gradational boundaries between the nodules and surrounding shale and on lack of evidence of transport of the nodules as clasts. Nodules are commonly severely corroded by weathering, with preferential dissolution of the central portion, and with rims rich in iron minerals.

Sedimentary structures are rare, and are restricted to the basal 12 cm of the section (field units A and B). Macroscopic structures include a wrinkled surface (runzelmarks?) at 6.8 cm (with long axes of wrinkles trending 024°) and two sets of primary current lineation at 8.5 cm (one trending 029° and the other trending 019°). Field units A and B also contain rare scour features. The thickest bed found in field unit B (20 mm thick, silty at base) is floored by a well-developed scoured sole surface with approximately 5 mm relief, and has a well bioturbated top.

Preservation of any sedimentary structures in the basal 6 cm (field unit A) and the uppermost 3 cm (field unit I) of the succession is unlikely due to the extensive bioturbation in these intervals (see below).

5.2. Bioturbation

Overall, the extent of bioturbation is variable across the studied interval, with significant infaunal mixing evident in the lower and uppermost parts of the section (ichnofabric index [i.i.] 4) bracketing an interval characterized by low extent of bioturbation (i.i. 1 to 2) and iron mineral replacement of discrete burrows and burrow networks (Fig. 4).

Within the basal 11 cm of the section, infaunal activity was relatively intense (i.i. 4), resulting in significant disruption of the primary bedding despite the relatively shallow maximum depth of bioturbation (15 mm) in this section. Some sclerites on the hash surfaces (see below) within this interval and also in the uppermost part of the section (40.5 cm to 43 cm) are orientated at oblique angles

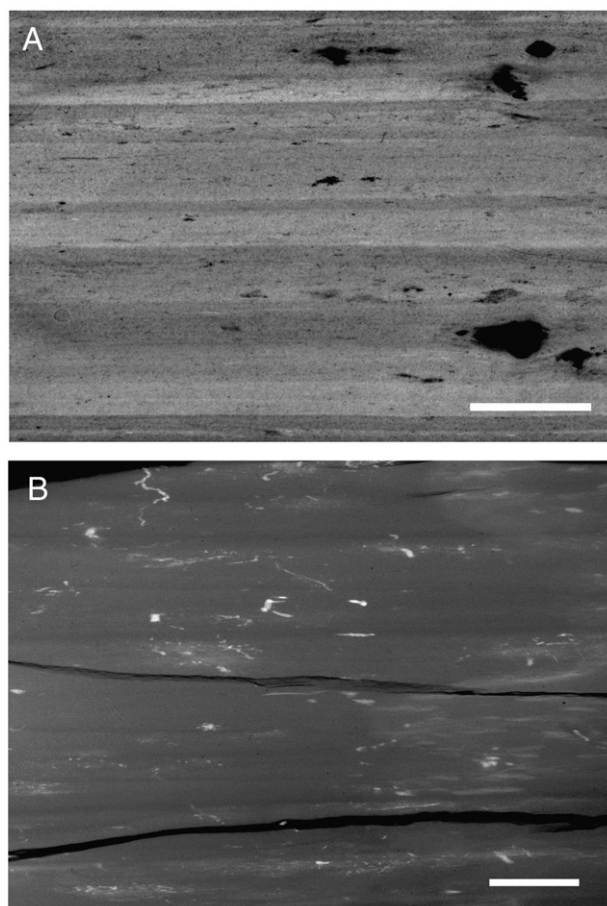


Fig. 5. A, Polished slab showing series of stacked clay beds. Represented strata are from 29 cm to 32 cm above the base of the section (field unit F; no carbonate nodules were encountered in this particular slab). Dark spots are iron oxide "blebs". See text for details. B, X-radiograph showing iron-filled, intricate, shallow burrow networks (light patches) in upper portions of clay beds (ichnofabric index 2). Represented strata are from 17 cm to 22 cm above the base of the section (field units C and D). Scale bars = 10 mm.

to the bedding. These sclerites may have been rotated from near-horizontal orientations by infaunal mixing, or may represent rapid deposition from a poorly organized flow. Most burrows in this part of the section are indistinct and visible only in polished slabs as disruptions of bedding, although simple horizontal, tubular trace fossils approximately 2 mm in diameter occur 7.5 cm above the base of the section.

The intensity of bioturbation declined significantly in the middle part of the section between 11 cm and 40.5 cm, where bed contacts are crisply defined (see above). This part of the section is characterized by i.i. 2, with the exception of an interval from 13–15.5 cm which contains no evidence of bioturbation (i.i. 1). Discrete burrows occurring in the middle part of the section are commonly filled with an iron oxide mineral. This mineral is interpreted to result from the weathering of pyrite, which formed in the burrows as linings or fillings during early diagenesis (see below). X-radiography revealed the presence of shallow networks of connected burrows less than 1 mm in diameter and 1 mm to 5 mm in depth at the tops of many depositional beds in this interval (Fig. 5b). Larger discrete vertical burrows up to 3 mm in diameter and 10 mm deep occur at 17.5 cm, 26 cm, and 40 cm above the base of the section.

Beds in the uppermost part of the section (40.5–43 cm) are extensively bioturbated (i.i. 4) and discrete burrows, where present, are not associated with iron mineral fillings. Throughout the entire section, burrow size and depth show strong correspondence with extent of bioturbation.

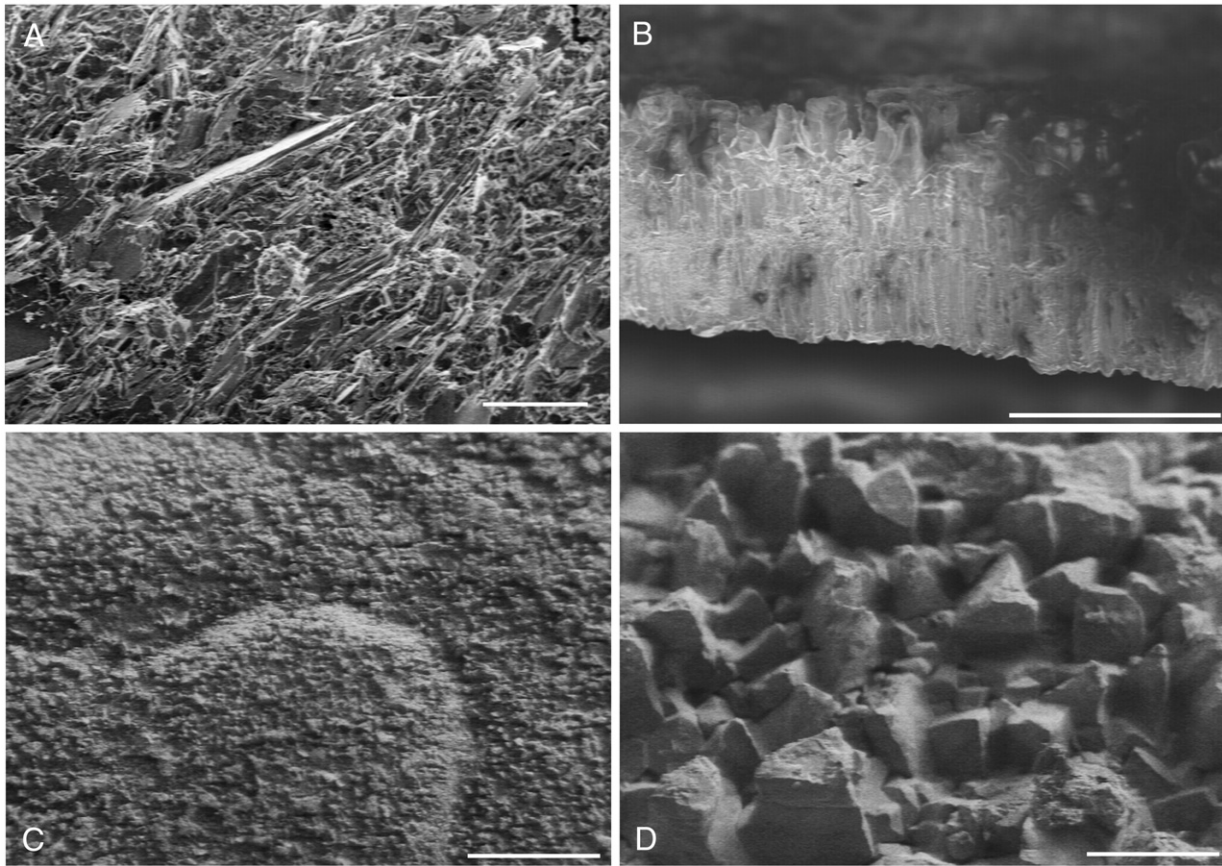


Fig. 6. A, SEM of claystone showing microfabric of randomly orientated clay particles. Sample taken from basal 6 cm of section, but typical of entire succession. Scale bar = 20 μm . B–D, SEM of a trilobite cephalon preserved within a calcite halo. B, Cross section. Elongate crystals (which grew inwards from the top and bottom) meet in the middle; there is no trace of the replaced trilobite sclerite. Scale bar = 200 μm . C, Dorsal view of anterior portion of cephalon (frontal lobe of glabella, preglabellar field, plectrum, and anterior cephalic border), with sagittal axis orientated top right to bottom left. Crystal size and orientation does not change across the sclerite boundary (top right). Scale bar = 500 μm . D, Details of blocky calcite crystals on replaced glabella. Scale bar = 50 μm .

5.3. Iron minerals

Iron oxides occur in great abundance within the section as discrete accumulations (“blebs”), burrow infillings, and in concentrations within carbonate nodules (described above). These modes of occurrence are characteristic of early diagenetic pyrite, which is readily oxidized to form iron oxide minerals (most importantly haematite or limonite–haematite) by meteoric waters during weathering. The recent mobilization and redistribution of iron compounds in Ruin Wash claystones is indicated by pervasive iron oxide stains on cleavage surfaces and around joints and fractures in the rock, which display a leisegang-type banding pattern that cuts across bedding.

Pyrite commonly forms during early diagenesis in marine sediments as a byproduct of microbial reduction of iron and sulphate under suboxic conditions. Pyrite-lined burrows and cavities are common in the rock record and are considered indicative of moderate sedimentation rates under dysaerobic bottom waters (Brett and Baird, 1986), an interpretation consistent with the ichnologic data in this case (the abundance of pyrite-lined burrow and cavities is inversely correlated with ichnofabric index).

The first occurrence of such discrete accumulations of iron oxides within the claystone matrix is at 10.6 cm to 10.8 cm above the base of the section (Fig. 4), closely associated with the pronounced decrease in intensity of bioturbation at 11 cm. Iron oxide burrow infillings are abundant in the interval from 11 to 39 cm (Fig. 5b), but do not occur higher than 39 cm above the base of the section.

Some trilobite moulds display a red or maroon iron staining which we infer was derived from weathering of pyrite. This staining extends beyond

the fossil material on many specimens (Fig. 7). All specimens exhibiting iron staining lie at or close to joint planes. Such staining exhibits a similar distribution to that of manganese dendrites in the section. The iron staining and the manganese dendrites are therefore uninformative as to the biostratinomic and early diagenetic history of the Ruin Wash Lagerstätte. The pervasive iron staining complicates the interpretation of X-radiographs, but does not impede the visibility of sedimentary features.

6. Trilobite biostratinomic details

Taphonomy may provide information on environmental conditions which are not attainable from sedimentological data alone (e.g., the “taphofacies” concept; Speyer and Brett, 1986, 1988, 1991; Brett and Baird, 1986, 1993; Brandt, 1989; Speyer, 1991; Brett et al., 1997; Hunda et al., 2006; see also Brett and Allison, 1998). Parameters such as the preservational mode, abundance, and taxonomic composition of bioclasts, the degree of articulation among sclerites of the multi-element trilobite exoskeleton, and the size distribution, orientation, dorso-ventral attitude, and degree of fragmentation of preserved remains are particularly informative (Brett and Allison, 1998). Study of such parameters yields insight into physical (e.g., the strength and direction of any water currents, sediment accumulation rate, seafloor oxygenation, bathymetry) and biological (e.g., predation, scavenging, bioturbation) processes/conditions which may have introduced non-random bias in the nature of fossil preservation, which in turn can lead to important palaeoecological and palaeobiological inferences (e.g., community composition, assemblage autochthoneity, organismal



Fig. 7. External mould of an articulated specimen of *Olenellus fowleri* showing iron staining related to recent weathering (FMNH PE57680). Scale bar = 10 mm. See text for details.

behaviour, etc.). Data regarding the various taphonomic parameters (Table 1) are presented in the following paragraphs, and are interpreted in the Inferred Depositional Environment section, below.

6.1. Trilobite preservation

Trilobites of the Ruin Wash Lagerstätte are typically preserved as high quality internal or external moulds (Fig. 2; Palmer, 1998a; Webster, 2007a) preserving fine details of exoskeletal ornament; others are preserved through mineral replacement as calcite (Figs. 6b–d and 8) or chlorite (Fig. 9) within claystones and as silica within carbonate nodules. Moulds displaying exoskeletal compaction-related fractures indicate that dissolution of the original exoskeleton must have occurred following compaction of the sediments during burial. Moulds commonly display a red or maroon iron staining derived from recent weathering of pyrite, as discussed above.

Calcite-replaced trilobite fossils occur within wafer-like “haloes” of cream-coloured calcite less than 0.5 mm thick from 12 cm to 39 cm above the base of the section (Fig. 8). Haloes have been observed around trilobite exoskeletal elements spanning many degrees of articulation, from fully articulated dorsal exoskeletons (Fig. 8a) to partially disarticulated exoskeletons (Fig. 8b), isolated cephalata (Fig. 8c), thoracic segments, and exoskeletal fragments (Fig. 8d). The haloes that are not restricted to specimens interpreted as carcasses suggest that halo growth was not dependent upon the presence of a large volume of organic remains. Haloes are typically sub-circular and centred upon a sclerite nucleus, although the nucleus is occasionally slightly off-centre. The presence of exoskeletal extensions such as genal spines on isolated cephalic nuclei is not reflected in the outline of the surrounding haloes. X-ray diffraction and SEM analyses indicate that the haloes are composed of aggregates of blocky crystals of calcite approximately 50 μm in size (Fig. 6d). The size and ordering of the crystals suggest that haloes grew by rapid precipitation under little confining pressure. The size and orientation of crystals (Fig. 6c) is consistent across haloes, with no difference in texture inside the margins of the sclerites compared to the calcite portion lying outside of the sclerite. Analysis of cross-sections of sclerite elements within haloes indicates that

sclerites were fully dissolved at the time of halo growth (Fig. 6b). Thus, the haloes did not grow on or around carbonate skeletal elements, but instead precipitated in and around void spaces left behind by the dissolution of sclerites. The haloes formed from carbonate-rich fluids that moved into the voids generated by the dissolution of sclerites. The $\delta^{13}\text{C}$ values of calcite haloes (–3.2 to –5.4‰; $n=9$) lie within the range of latest Early Cambrian seawater values reported by Montañez et al. (2000). Thus the carbon isotopic composition of the haloes indicates that the carbonate was derived from local dissolution and re-precipitation of carbonate rather than from diagenetic mineralization of organic carbon. Carbonate may have been derived from the ribbon limestones immediately overlying the interval, from carbonate nodules within and above the interval, or possibly from the original sclerites, all of which would be expected to have $\delta^{13}\text{C}$ values similar to seawater. Whether the precipitation of haloes was a Cambrian event or occurred during the Quaternary is uncertain.

Sclerites within the haloes show evidence of compaction-related fracturing consistent with fracture patterns shown by trilobite fossils preserved as moulds. The haloes therefore must have been emplaced following compactional deformation of fossils. The distribution of haloes on fracture planes which may lie slightly oblique to bedding strongly suggests that the haloes formed as a result of recent weathering in the shallow subsurface, and not as a result of Cambrian diagenetic processes.

Chlorite-replaced trilobite fossils also occur in the section and appear black in cross-section and on bedding planes. A chlorite composition of the replacing black material was identified using thin sections and SEM-EDS spot analyses. Like calcite-replaced sclerites, chlorite-replaced fossils may occur on bedding planes with non-replaced, mouldic fossils. Trilobite sclerites replaced by chlorite also occur in the Burgess Shale, wherein chloritization of skeletal fossils has been shown to result from greenschist-phase metamorphism (Butterfield et al., 2007). A metamorphic origin is excluded for chloritic fossils from Ruin Wash, however, as XRD analysis of clay mineral separates revealed that only the clay mineral illite is present in the matrix: metamorphism would have resulted in transformation of illite to chlorite and muscovite. Thin-section analysis reveals a void-filling habit of chlorite crystals (Fig. 9). Thus, chlorite replacement of sclerites also occurred following dissolution of primary calcite. Whether this replacement resulted from early diagenetic processes in the burial environment or from recent weathering in the shallow subsurface is uncertain.

Trilobites occur rarely within carbonate nodules at the top of field unit E and in field units G through I, which also contain inarticulate brachiopods retaining an original phosphatic composition. Trilobite sclerites preserved in these nodules are replaced by silica, and exhibit excellent three-dimensional preservation compared to compacted specimens preserved in claystones (cf. Webster and Hughes, 1999) indicating that the nodules formed in the early burial environment, maintaining the form of the fossils prior to sediment compaction. Subsequently, the sclerites were dissolved and replaced by silica, which may have been released to pore waters by the dissolution of sponge spicules or the diagenesis of clay minerals.

6.2. Bioclast abundance

The stratigraphic distribution of trilobite bioclasts throughout the 43 cm section is non-uniform. On some surfaces, bioclasts are densely packed (often in point contact or overlapping), forming a distinct pavement of exoskeletal remains (Fig. 10). Such pavements are here termed “hash surfaces” on account of the high degree of disarticulation of trilobite sclerites preserved on them, although articulated remains were occasionally encountered (e.g., Fig. 10d; see below). Hash surfaces represent the densest bioclast accumulations within the succession. Most sclerites on hash surfaces lie parallel or subparallel to bedding; a minority lie at oblique orientations, perhaps tilted through bioturbation (see above). Single pavements up to 5 mm thick (after compaction) were observed. Sclerites on at least some hash surfaces show a weak preferred orientation (see below).

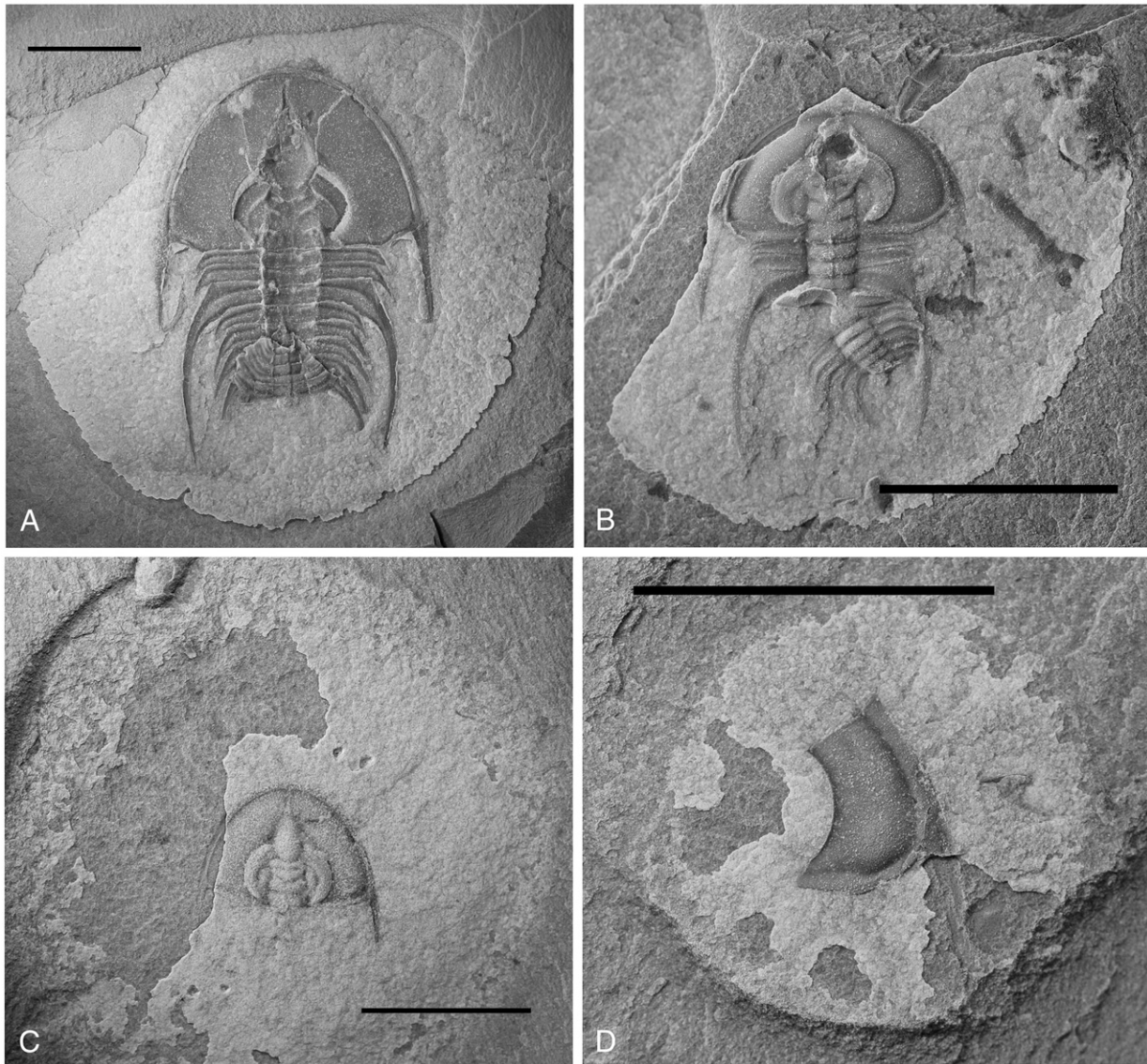


Fig. 8. Trilobite bioclasts preserved within calcite haloes. A, Articulated dorsal exoskeleton (cephalon plus prothorax) of *Olenellus chiefensis* (UCR 9945.22). The posteriormost prothoracic segments are inverted relative to the rest of the trunk and cephalon. B, Partially disarticulated dorsal exoskeleton of *Olenellus gilberti* (UCR 9945.71). C, Isolated cephalon of *O. chiefensis* (UCR 9945.65). D, Fragment of an olenelloid cephalon preserved within a calcite halo (same slab as UCR 9945.65). Scale bars = 10 mm.

Hash surfaces are abundant in the basal 6 cm of the section (field unit A), where they form irregular and often amalgamating surfaces deformed by the interspersed compaction-resistant carbonate nodules. The frequency of hash surfaces then markedly drops (Fig. 4): a single, thin hash surface occurs 8.8 cm above the base of the section (field unit B) and a minor, discontinuous hash surface was found at 22.5 cm above the base of the section (field unit D). A distinct hash surface at 23.5 cm above the base of section (“Surface 1” on Fig. 4 and in subsequent discussion) separates field unit D from the overlying unit E. Field unit E contains a hash surface at 26 cm and is capped by another (29 cm; “Surface 2” on Fig. 4 and in subsequent discussion). A hash surface also caps field unit F (31.5 cm; “Surface 3” on Fig. 4 and in subsequent discussion); the surface undulates with up to 1 cm of relief due to the underlying carbonate nodules. Hash surfaces up to 5 mm thick occur above (35.5 cm) and below (33.5 cm) the layer of carbonate nodules in field unit G. Hash surfaces are abundant above 38.5 cm (top portion of field unit H and throughout unit I), becoming more frequent up-section where they take an irregular and amalgamated form similar to that seen in unit A.

A layer of abundant, densely packed, filamentous, dark organic debris, probably representing algal remains, was found at 25.7 cm above

the base of the section (within field unit E). The debris was typically comminuted into fine fragments, although some pieces were almost 10 mm long. Whether this layer represents a hash surface rich in nonmineralized organic remains (rather than trilobite bioclasts) is unclear. Similar organic debris was observed dispersed at lower abundance on slabs extracted from other Ruin Wash trenches. Preservation of such nonmineralized fossils at Ruin Wash will be discussed elsewhere.

Bioclast abundance varies along and among hash surfaces (Fig. 10). A total of 36 bioclasts were found within a 15 cm by 15 cm quadrat placed randomly on Surface 1 (Fig. 10d); three randomly placed quadrats on Surface 2 (Fig. 10a–c) sampled 42, 29, and 16 bioclasts, respectively; and Surface 3 was entirely covered with partially-overlapping sclerites. Four randomly placed quadrats on Surface 3 sampled 19, 40, 42, and 42 clearly visible bioclasts, respectively, excluding the mostly-obscured material. Hash surfaces in unit G were similarly densely packed with sclerites in point contact.

Relative to their abundance on hash surfaces, bioclasts are sparsely distributed throughout the rest of the claystone units. Quadrats placed randomly on surfaces 8 cm and 10 cm above the base of the section (in field unit B) failed to sample any bioclasts, and a total of only 42 bioclasts

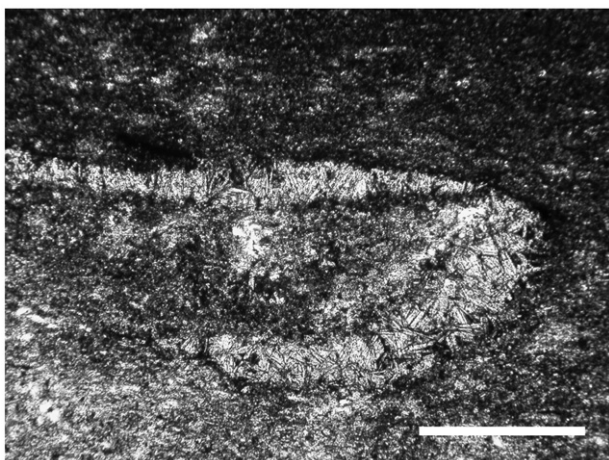


Fig. 9. Cross section through trilobite preserved by chlorite replacement, showing void-filling habit of chlorite crystals. Scale bar=0.5 mm. See text for details.

were recovered from the 6 cm-thick unit as a whole. Within the overlying field unit C (5.5 cm thick) some 113 trilobite bioclasts were recovered, although the average concentration was again low; a quadrat

placed randomly on a surface 13.5 cm above the base of the section failed to sample any bioclasts, and three quadrats placed randomly on a surface 16.0 cm above the base of the section sampled 2, 5, and 8 bioclasts, respectively. Within field unit D (6 cm thick; 68 bioclasts recovered), specimens were scattered with an average concentration of approximately one per 15 cm² of exposed surface; three quadrats placed randomly on a surface 20.5 cm above the base of the section sampled 0, 4, and 4 bioclasts, respectively. Only 24 bioclasts were recovered from field unit E (5.5 cm thick), with an average concentration of approximately 3 specimens per quadrat (ranging from 0 to 9). The prevalence of carbonate nodules and undulating hash surfaces in the thin field units F, G, H, and I precluded recovery of bioclasts from the entombing claystone.

Recognition of individual clay beds (above) within field units C through G in the field is rendered impossible owing to the uniform grain size, and the position of most trilobite bioclasts (i.e., at the base, in the middle, or at the top) within any clay bed could not be determined. However, analysis of polished slabs and thin sections reveal that bioclasts and hash surfaces are consistently located between or in the bases of discrete depositional beds.

Several slabs collected from the Lagerstätte but out of precise stratigraphic context reveal that articulated cephalothoraces sometimes occur in small clusters on particular surfaces (e.g., Fig. 2a, b), interpreted

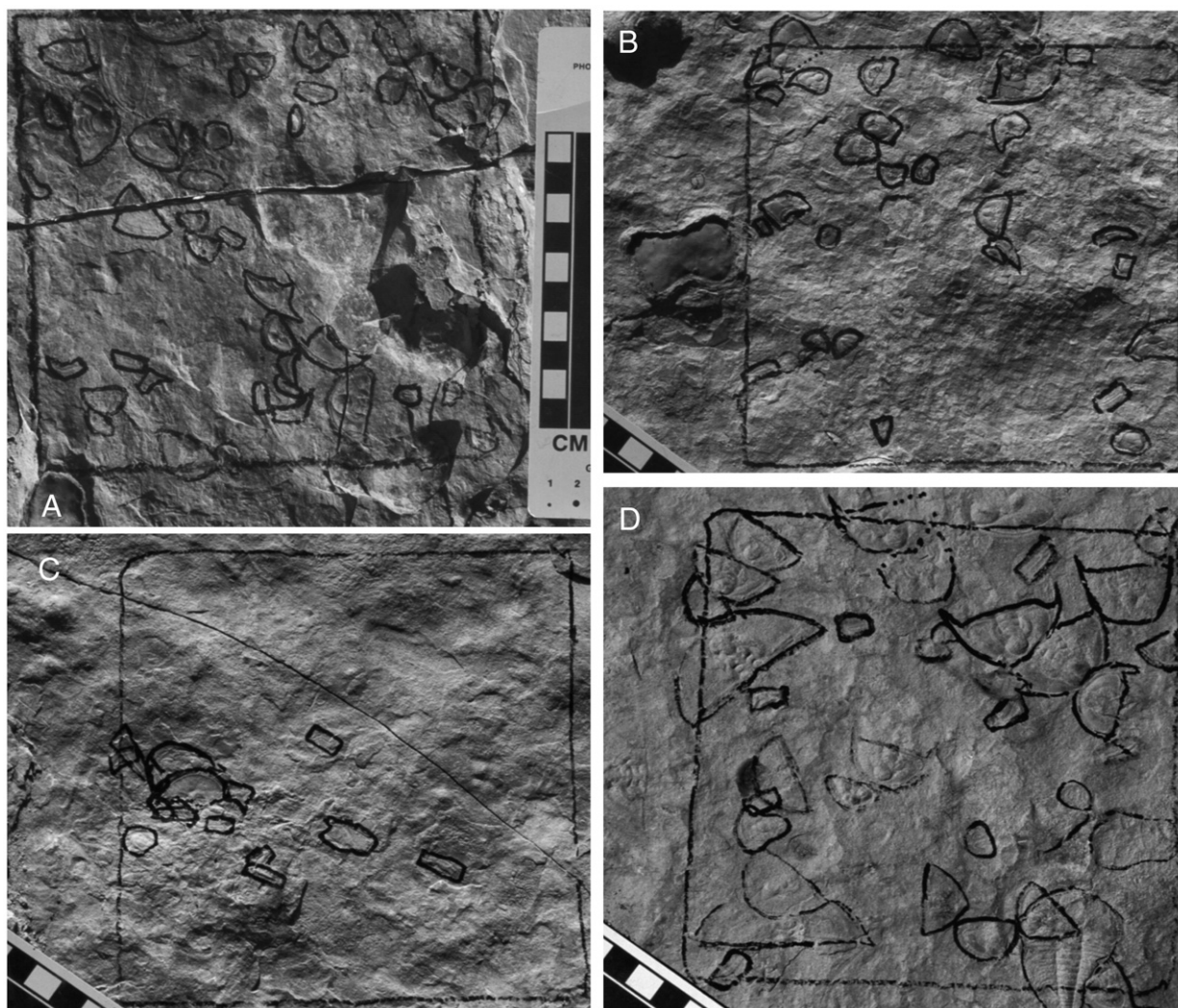


Fig. 10. Bioclast distribution and condition on hash surfaces, photographed in the field. Virtually all bioclasts are disarticulated (but note the articulated trilobite in the bottom right corner of D). A–C, Bioclast sampling within three 15 cm by 15 cm quadrats ($n=42$, 29, and 16, respectively) placed randomly on hash Surface 2 (29 cm above base of section; see Fig. 4). Note spatial clustering of bioclasts in C, D, Bioclast sampling ($n=36$) within a 15 cm by 15 cm quadrat placed randomly on hash Surface 1 (23.5 cm above base of section; see Fig. 4). Scale bar is orientated north–south in all photographs.

Table 2

Taxonomic composition through units of the Ruin Wash Lagerstätte, based on identification of isolated cephalons (fragmented and complete) plus cephalothoraxes (i.e., cephalons with associated thoracic segments)

Taxon	Unit B	Unit C	Unit D	Surface 1	Unit E	Surface 2	Surface 3
<i>O. gilberti</i>	8 (44%)	37 (46%)	18 (39%)	13 (45%)	17 (77%)	23 (48%)	24 (25%)
<i>O. fowleri</i>	0	3 (4%)	8 (17%)	4 (14%)	0	0	2 (2%)
<i>O. chiefensis</i>	1 (6%)	12 (15%)	13 (28%)	5 (17%)	3 (14%)	5 (10%)	9 (9%)
<i>O. terminatus</i>	4 (22%)	10 (12%)	1 (2%)	1 (3%)	2 (9%)	3 (6%)	6 (6%)
<i>N. geniculatus</i>	4 (22%)	12 (15%)	4 (9%)	1 (3%)	0	6 (13%)	7 (7%)
<i>B. brevispinus</i>	0	1 (1%)	0	0	0	0	2 (2%)
<i>Olenellus</i> sp.	1 (6%)	5 (6%)	2 (4%)	5 (17%)	0	9 (19%)	36 (38%)
<i>Zacanthopsis</i> sp.	0	1 (1%)	0	0	0	0	0
Unidentifiable	0	0	0	0	0	2 (4%)	9 (9%)
Total	18	81	46	29	22	48	95

Percentages given to nearest integer.

below. Weathering of the slabs has obscured bedding structures, and the slabs cannot be correlated into the measured section based on clay bed thicknesses; nor is it possible to determine whether the slabs hail from one surface or from multiple beds. However, absence of silt-sized grains, hash surfaces, and carbonate nodules from the slabs indicates provenance from somewhere between 12 cm and 29 cm above the base of the section (field units B through E). No obvious clusters of articulated cephalothoraxes were encountered in the “taphonomy trench”, although this likely results from the patchy spatial distribution of the clusters on the surface(s). The clusters are characterized by a dominance of articulated cephalothoraxes (many interpreted as carcasses, based on exoskeletal completeness and retention of a hypostome in life position) over disarticulated sclerites and are therefore considered distinct from hash surfaces, even though specimens within a cluster may be in point contact (see interpretation section below).

6.3. Taxonomic composition

The six olenelloid species which commonly occur in the Ruin Wash Lagerstätte (above) are also known from correlative strata at many localities around the southern Great Basin (Palmer, 1998a; Fowler, 1999; Webster et al., 2003; Webster, 2007a, b; unpublished data). The Ruin Wash trilobite fauna is therefore unusual in preservational quality but not in composition. All six species occur in horizons

Table 3

Taxonomic composition through units of the Ruin Wash Lagerstätte, based on identification of isolated cephalons (fragmented and complete) only

Taxon	Unit B	Unit C	Unit D	Surface 1	Unit E	Surface 2	Surface 3
<i>O. gilberti</i>	8 (44%)	34 (46%)	14 (37%)	12 (43%)	16 (76%)	23 (48%)	24 (25%)
<i>O. fowleri</i>	0	3 (4%)	7 (18%)	4 (14%)	0	0	2 (2%)
<i>O. chiefensis</i>	1 (6%)	12 (16%)	12 (32%)	5 (18%)	3 (14%)	5 (10%)	9 (9%)
<i>O. terminatus</i>	4 (22%)	10 (14%)	1 (3%)	1 (4%)	2 (10%)	3 (6%)	6 (6%)
<i>N. geniculatus</i>	4 (22%)	8 (11%)	2 (5%)	1 (4%)	0	6 (13%)	7 (7%)
<i>B. brevispinus</i>	0	1 (1%)	0	0	0	0	2 (2%)
<i>Olenellus</i> sp.	1 (6%)	5 (7%)	2 (5%)	5 (18%)	0	9 (19%)	36 (38%)
<i>Zacanthopsis</i> sp.	0	1 (1%)	0	0	0	0	0
Unidentifiable	0	0	0	0	0	2 (4%)	9 (9%)
Total	18	74	38	28	21	48	95

Percentages given to nearest integer.

Table 4

Taxonomic composition through units of the Ruin Wash Lagerstätte, based on identification of articulated cephalothoraxes (i.e., cephalons with associated thoracic segments) only

Taxon	Unit B	Unit C	Unit D	Surface 1	Unit E	Surface 2	Surface 3
<i>O. gilberti</i>	0	3 (43%)	4 (50%)	1 (100%)	1 (100%)	0	0
<i>O. fowleri</i>	0	0	1 (13%)	0	0	0	0
<i>O. chiefensis</i>	0	0	1 (13%)	0	0	0	0
<i>O. terminatus</i>	0	0	0	0	0	0	0
<i>N. geniculatus</i>	0	4 (57%)	2 (25%)	0	0	0	0
<i>B. brevispinus</i>	0	0	0	0	0	0	0
<i>Olenellus</i> sp.	0	0	0	0	0	0	0
<i>Zacanthopsis</i> sp.	0	0	0	0	0	0	0
Unidentifiable	0	0	0	0	0	0	0
Total	0	7	8	1	1	0	0

Percentages given to nearest integer.

stratigraphically below the base of the Lagerstätte (Palmer, 1998a; Webster, 2007a,b; unpublished data) and in the stratigraphically highest well-sampled interval (Surface 3) of the “taphonomy trench” at Ruin Wash (Table 2); silicified specimens of *Nephrolenellus geniculatus*, *Olenellus* sp., and an oryctocephalid were also recovered from carbonate nodules as high as the top of field unit G. The olenelloid species are therefore known to range through the time interval represented by the bulk of the Ruin Wash Lagerstätte (field units A through F or G, inclusive).

Identification of all sampled cephalons (irrespective of degree of fragmentation and association with thoracic segments) reveals that *Olenellus gilberti* consistently dominates the trilobite fauna in all units and surfaces of the Ruin Wash Lagerstätte (Table 2). *Olenellus chiefensis* typically ranks second in abundance, although *Olenellus terminatus* and/or *Nephrolenellus geniculatus* are more abundant within field units B and C and on hash Surface 2. *Olenellus fowleri* is relatively rare except in field unit D and on hash Surface 1. *Bolbolellus brevispinus* and *Zacanthopsis* sp. represent the rarest elements of the trilobite fauna recovered from the siliciclastics, and were found only in intervals from which the largest sample sizes of bioclasts were recovered (field unit C and hash Surface 3; Table 2), emphasizing the need for large sample size in assessments of diversity. The oryctocephalid was recovered only from the carbonate nodules, and three additional trilobite species known to occur extremely rarely at Ruin Wash (listed above) were not recovered from the “taphonomy trench”. Poorly preserved, highly incomplete, or mostly obscured cephalons which could not be identified to species and/or genus level (“*Olenellus* sp.” and “Unknown” in Table 2) are common only on hash surfaces.

Articulated cephalothoraxes (i.e., cephalons with associated thoracic segments) were rarely sampled in the “taphonomy trench”. However, the limited data suggest that there might be a taxonomic bias in the preservation of articulated specimens. Compared to the proportional abundance within the trilobite fauna based on occurrence of isolated

Table 5

Bioclast composition through units of the Ruin Wash Lagerstätte

	Articulated sclerites			Isolated sclerites			Frequency of articulated specimens (%)
	Total	CTX	ATS	C	HYP	TS	
Unit B	42	0	2	18	2	20	0
Unit C	113	7	3	74	0	29	9
Unit D	68	8	4	38	2	16	17
Surface 1	36	1	0	28	0	7	3
Unit E	24	1	1	21	0	1	5
Surface 2	87	0	0	48	5	34	0
Surface 3	143	0	0	95	2	46	0
Totals	513	17	10	322	11	153	5

Sclerite abbreviations: ATS, articulated thoracic segments; C, cephalon; CTX, cephalothorax; HYP, hypostomes; TS, thoracic segments.

represented and articulated specimens of *Nephrolenellus geniculatus* are over-represented (Tables 3 and 4). The small sample size inhibits statistical testing for this potential bias. Taxonomic differential in susceptibility to disarticulation has been noted in Silurian trilobites (Mikulic, 1990).

6.4. Bioclast composition

The multi-element trilobite exoskeleton can provide useful biostratigraphic information given its propensity to disarticulate into its component sclerites through physical (e.g., current action) or biological (e.g., predation/

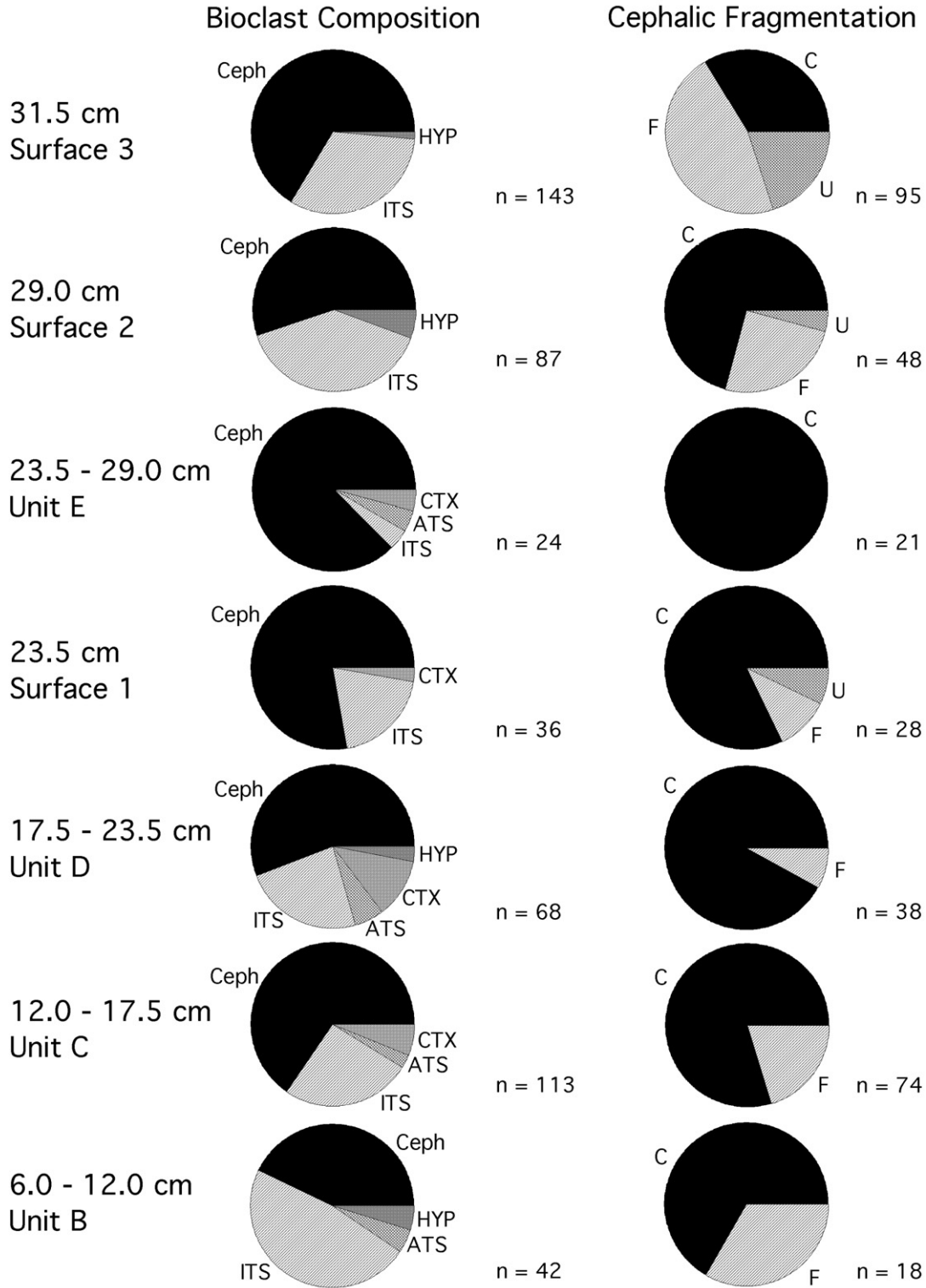


Fig. 11. Pie charts summarizing bioclast composition (left column; see also Table 5) and relative frequency of fragmentation among isolated cephalons (right column; see also Table 7) through the Ruin Wash Lagerstätte. Abbreviations for bioclast composition: Ceph, isolated cephalons; ITS, isolated thoracic segments; ATS, articulated thoracic segments; CTX, articulated cephalothorax; HYP, hypostome. Abbreviations for bioclast fragmentation: C, complete cephalon; F, fragmentary cephalon; U, condition of cephalon uncertain. See text for details.

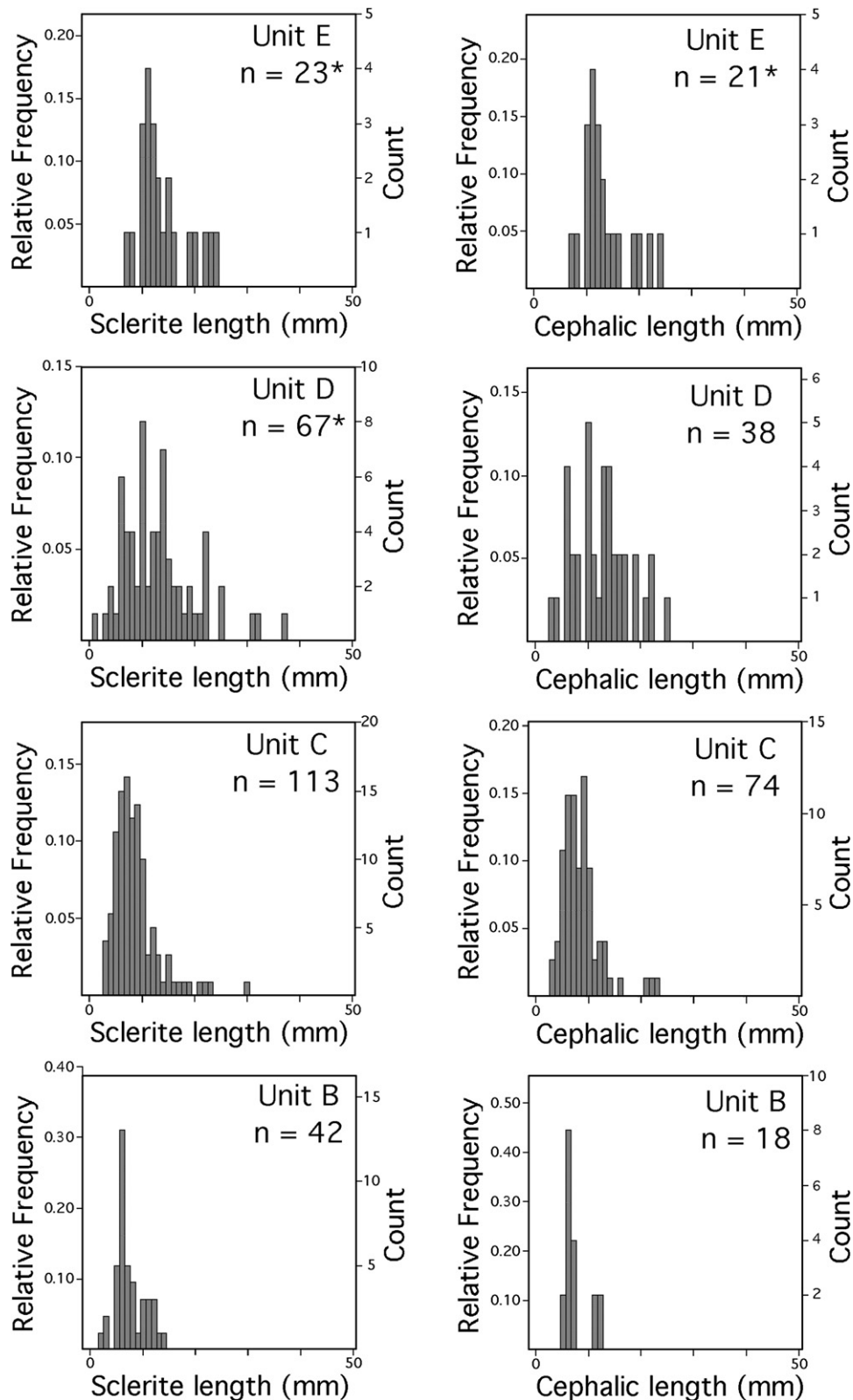


Fig. 12. Size frequency distribution of all sclerites (left column) and isolated cephalae (right column) through units of the Ruin Wash Lagerstätte (excluding hash surfaces). An asterisk after the sample size indicates that bioclasts larger than 50 mm in length were excluded from the plot. See text for details.

scavenging, decay, bioturbation) processes. The disarticulated sclerites can in turn be shape- or size-sorted by physical processes (see below). The ratio of articulated to disarticulated skeletal components in arthropods has been proposed as a general index of background burial rates and/or reworking (Westrop, 1986; Speyer, 1987; Speyer and Brett, 1986, 1988).

Almost 95% of trilobite clasts recovered from the “taphonomy trench” were isolated sclerites (Table 5). The proportion of bioclasts retaining some degree of articulation varied through the section (Table 5; Fig. 11). The stratigraphically lowest articulated specimens (runs of 4 and 5 thoracic segments) were found within field unit B (6 to 12 cm above

the base of the section). The lowest articulated cephalothorax was found 13 cm above the base of the section (field unit C). No articulated trilobite remains were recovered above field unit E. The proportion of cephalothoraces relative to the total number of cephalata (isolated plus those with associated thoracic segments) is lowest on hash surfaces (3%, 0%, and 0% on Surfaces 1, 2, and 3, respectively). Articulated material was also rare on the hash surface within field unit E (26 cm above the base of the section). Field units B through D contain a progressively increasing proportion of cephalothoraces relative to the total number of cephalata (0%, 9%, and 17%, respectively); the proportion then drops to 5% in the overlying unit E. A similar pattern is found when considering the proportion of articulated bioclasts (cephalothoraces plus runs of thoracic segments) relative to the total number of bioclasts (data not shown).

Thoracic segments and hypostomes are clearly under-represented relative to cephalata in all units and on all hash surfaces (Table 5). Although some of these smaller sclerites may have been overlooked during sampling, the magnitude of the under-representation suggests that the assemblage was subject to some size- or shape-sorting prior to burial (see Inferred Depositional Environment below). Olenelloid pygidia are strongly micropygous and known for very few species: their general rarity may result from sampling bias, size- or shape-sorting, or (speculatively) weak biomineralization and low preservation potential. [Non-uniform biomineralization of the exoskeleton is known to occur in one of the Ruin Wash olenelloids, *Bolbolenellus brevispinus* (see Palmer, 1998a).] Rare, pygidium-bearing articulated olenelloids are known from Ruin Wash (Palmer, 1998a; Fig. 2d), but none were recovered from the “taphonomy trench”. Analogously, differential thickness (and presumably preservation potential) among sclerites is evident in a species of the Ordovician trilobite *Gravicalymene*, the hypostome of which was approximately half as thick as the exoskeleton of the cranidium and thoracic segments (Hughes and Cooper, 1999, Fig. 6).

Although not recovered from the “taphonomy trench”, clusters of articulated cephalothoraces (Fig. 2a, b; see above, interpreted below) reveal that the distribution of articulated remains is also spatially patchy on at least one surface.

6.5. Bioclast size distribution

Current activity can lead to sorting of trilobite sclerites by shape or by size (Speyer, 1983; Westrop, 1986; Hesselbo, 1987). A wide size range of bioclasts are preserved within each of the various units and hash surfaces of the Ruin Wash Lagerstätte (Figs. 12 and 13). The minimum size of sampled sclerites was 1 to 3 mm in most intervals, although hash Surface 1 and field unit E had larger minimum sclerite sizes (6 mm and 7 mm, respectively).

The relative scarcity of very small bioclasts may result from biostratinomic processes (e.g., current-sorting) or from sampling bias (small sclerites are more easily overlooked). Laboratory examination of hundreds of Ruin Wash claystone slabs using a microscope confirms that morphologically immature cephalata with sagittal cephalic lengths <2 mm are relatively scarce, suggesting that any sampling bias in the bioclast size distributions reported here (based on data collected in the field) is slight.

The maximal size of trilobite bioclasts recovered differed widely across units. Maximum observed bioclast size on hash surfaces (42 mm, 22 mm, and 30 mm for Surfaces 1, 2, and 3, respectively) was typically smaller than the maximum bioclast size observed within units (excluding hash surfaces). The trend in maximal bioclast size within units mirrors the trend in the proportion of articulated bioclasts (above), increasing from units B through D (14 mm, 30 mm, and 90 mm, respectively), then decreasing to 60 mm in unit E. (Bioclasts up to 40 mm, 20 mm, and 20 mm long were observed in units G, H, and I, respectively, although the abundance of carbonate nodules precluded collection of detailed biostratinomic data.) The coupling of trends in frequency of articulation and maximal bioclast size is perhaps not

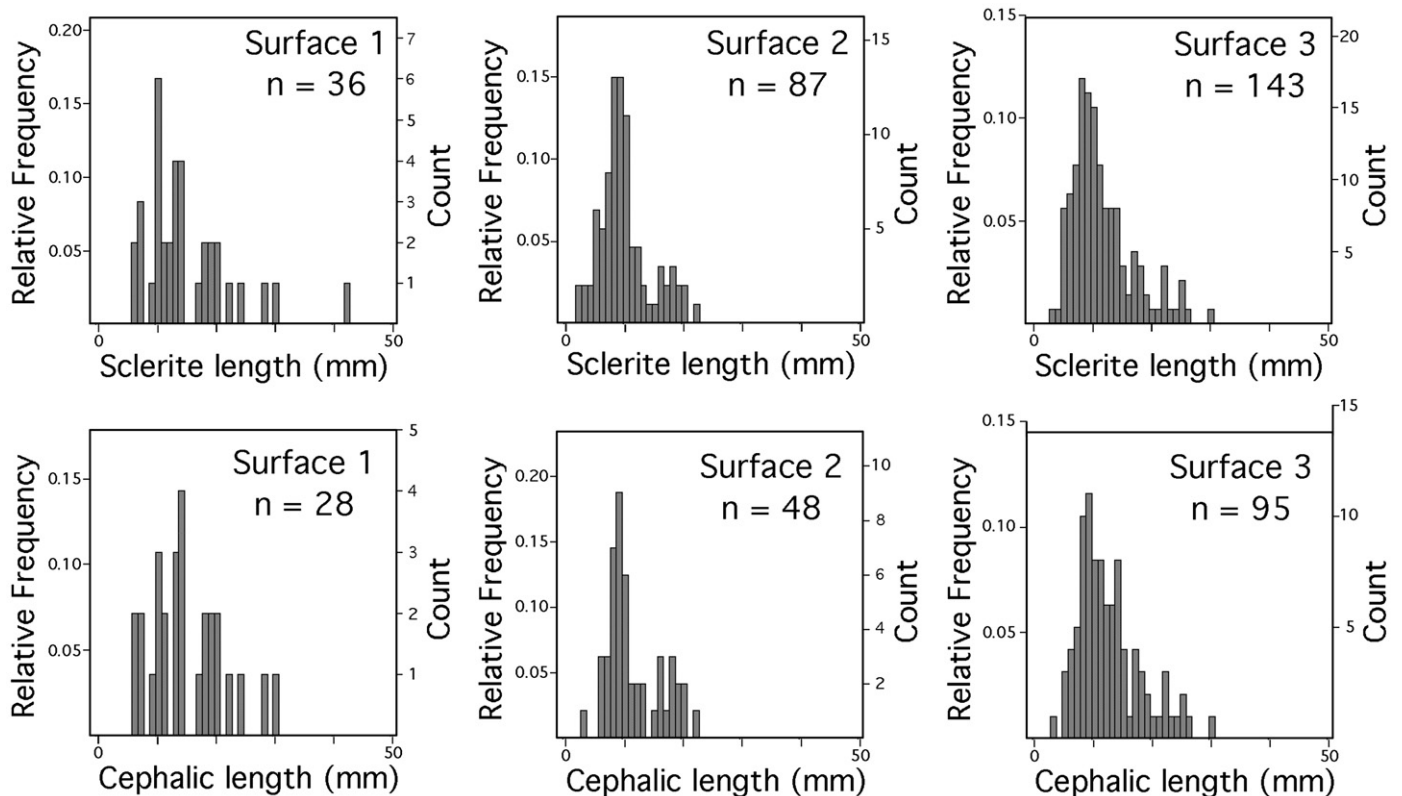


Fig. 13. Size frequency distribution of all sclerites (top row) and isolated cephalata (bottom row) on hash surfaces of the Ruin Wash Lagerstätte.

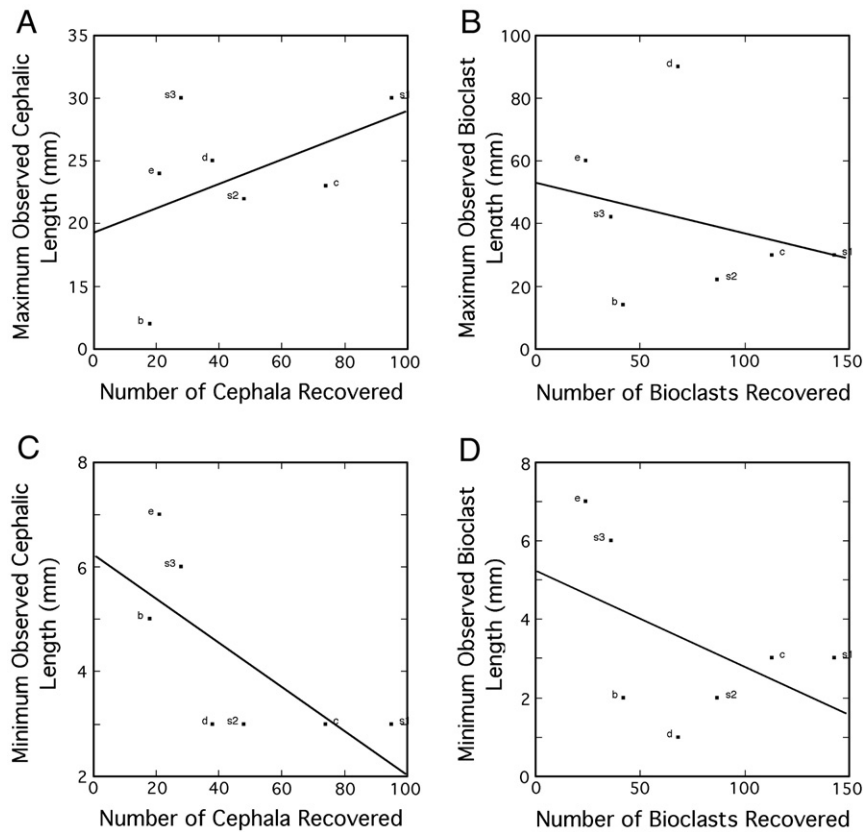


Fig. 14. Relationship between sample size and observed maximal (A, B) and minimal (C, D) bioclast size through units of the Ruin Wash Lagerstätte. A, C, Data for isolated cephalia only. B, D, Data for all bioclasts. Data points are identified by field unit (b, c, d, and e) and hash surface (Surface 1 = s1, Surface 2 = s2, and Surface 3 = s3) labels. Linear regression line is fitted for illustrative purposes only. See text for details.

surprising, because articulated bioclasts might be expected to be larger than isolated sclerites. However, the maximal size of isolated cephalia (Figs. 12 and 13) shows a similar trend, increasing from units B through D (12 mm, 23 mm, and 25 mm, respectively), then decreasing to 24 mm in unit E. The maximal size of isolated cephalia on hash surfaces (30 mm, 22 mm, and 30 mm on Surfaces 1, 2, and 3, respectively) closely matches or exceeds the maximal size of isolated cephalia in unit D.

The among-unit differences in bioclast abundance (above) raise the concern that among-unit differences in bioclast size maxima and minima are purely a function of contrasting sample size; if so, this would obviously limit the biostratigraphic inferences that could be drawn from such data. However, this does not appear to be the case, at least for maximal bioclast size. Although the null expectation of a positive correlation between number of isolated cephalia recovered from a unit and maximum size of isolated cephalia within that unit is met (Fig. 14a), the trend is driven almost entirely by the low values for each variable from unit B; indeed, a weakly negative correlation is found when all bioclasts are considered (Fig. 14b). The observed relationship between sample size and minimum bioclast size meets the null expectation of a negative correlation (albeit nonlinear) whether just isolated cephalia (Fig. 14c) or all bioclasts (Fig. 14d) are considered.

Curiously, the clusters of articulated cephalothoraces preserved on slabs of uncertain stratigraphic provenance (see above; Fig. 2a, b) comprise almost exclusively of large (>20 mm long, often much larger) exoskeletons; only rarely are smaller individuals and isolated sclerites found associated with them. Such clusters may represent the most extreme degree of size-sorted assemblage in the

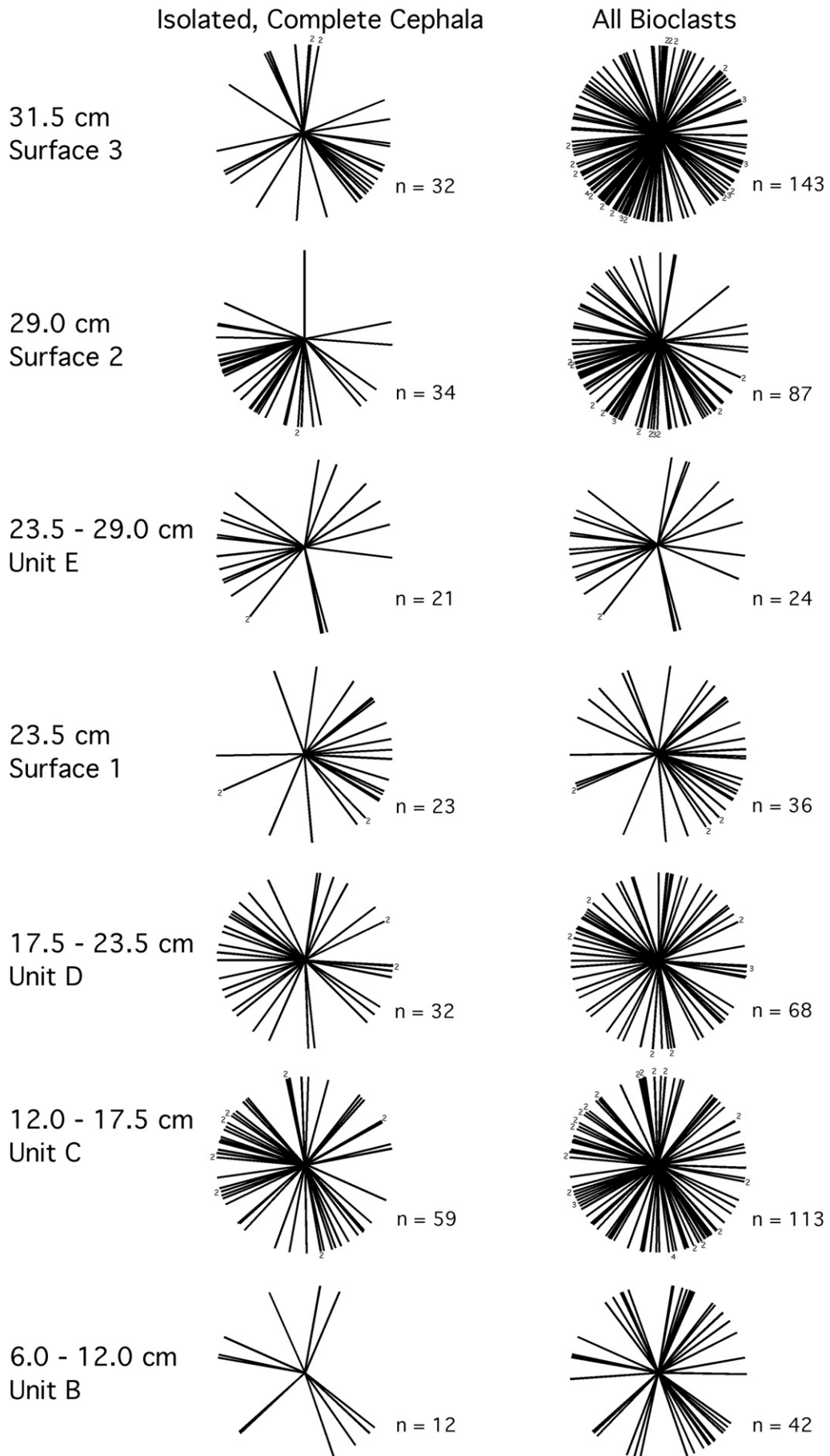
Ruin Wash Lagerstätte, although an ecological/behavioural explanation for the size distribution is deemed more likely (see interpretation below).

6.6. Bioclast orientation

Common alignment in the azimuth orientation of trilobite bioclasts can provide an indication of current or wave transportation. This is true for the long axes of articulated exoskeletons (Brett and Baird, 1986) and for isolated sclerites. Unidirectional current activity will reorientate an isolated complete (unfragmented) cephalon such that its sagittal axis is aligned with the current direction (anterior end pointing upcurrent), or such that its sagittal axis is perpendicular to the current direction, with the lateral margin facing into the current (Lask, 1993). Although the hydrodynamic properties of other sclerites have received less study, it might be expected that isolated thoracic segments align with their transverse axes parallel to the current. The response of fragmentary sclerites to a unidirectional current is unknown, and is likely to depend on the shape of the fragment. Orientation data are presented here for isolated complete cephalia and for all trilobite bioclasts (Fig. 15). Although these data sets are nested (the former being a subset of the latter), they sometimes lead to different inferences as to the presence/absence and direction of any preferred orientation (below). Such differences are likely attributable to sclerite- or fragmentation-specific response to currents.

Except for hash surfaces, data for bioclast orientation have been binned into the field units defined above. As noted above, each unit consists of numerous clay beds. Any changes in current direction among

Fig. 15. Orientation (relative to present-day north) of isolated, complete cephalia (left column) and all bioclasts (right column) through field units of the Ruin Wash Lagerstätte (see Fig. 4). Small numbers specify number of specimens represented by a vector (not specified when $n=1$). See text for details.



clay beds within a unit will be “analytically time-averaged” (cf. Behrensmeier and Hook, 1992) when orientation data for the unit as a whole are assessed. Lack of strong preferred orientation within a unit may therefore reflect either (1) genuine absence of currents sufficiently strong to reorientate bioclasts, or (2) relatively high frequency changes in current direction among clay beds within a unit, so that the current direction is not unidirectional at the scale of the whole unit. Subdivisions within field unit C (Fig. 16; below) highlight this problem.

There is no obvious preferred orientation among isolated complete cephalia within field unit B (although sample size is low), but there appears to be slightly denser occupation in the NNE and SSE directions when all bioclasts are considered (Fig. 15). The weakly supported NNE trend matches the orientation of the long axes of the wrinkles and primary current lineations preserved within the unit (see above).

When all bioclasts recovered from field unit C (12 cm to 17.5 cm above the base of the section) are considered together ($n=113$) no preferred alignment is apparent. Isolated complete cephalia from this unit ($n=59$) show a weak preferred alignment to the SSE and NW (Fig. 15). However, finer subdivision of data from within this unit reveals the potential for subtle changes in preferred orientation (Fig. 16). Thus, bioclasts in the basal 0.2 cm of unit C appear to show preferred orientations in approximately ENE, SSE, and WSW directions, although sample size is low. Two sclerites recovered at 12.5 cm above the base of the section are aligned roughly N and S (no complete cephalia were recovered from this horizon). Bioclasts recovered between 12.5 cm and 13.5 cm above the base of the section appear to show preferred orientations in approximately E, SSE, and SW directions, although sample size is again low. Bioclasts (including isolated complete cephalia) show broadly preferred alignment towards the NW and SE quadrants 14 cm above the base of the section, and those (including isolated complete cephalia) recovered from 16 cm above the base of the section may show weak preferred alignment towards the NW quadrant.

There is no obvious preferred alignment of sclerites (or just isolated complete cephalia) in field unit D (17.5 cm to 23.5 cm above the base of the section) as a whole (Fig. 15). Bioclasts (including isolated complete cephalia) recovered from field unit E are preferentially aligned to the NE and SW-to-NW quadrants, with a possible weak trend also to the SSE (Fig. 15). No obvious preferred alignment of bioclasts was noted when excavating through units G or H, although detailed taphonomic data could not be recorded.

The clustered cephalothoraces preserved on isolated slabs of uncertain stratigraphic provenance seem to show some degree of alignment, often in two roughly orthogonal directions (Fig. 2a, b). However, the cluster-bearing slabs were collected out of precise stratigraphic context, and azimuthal orientations could not be taken on the specimens for comparison to the data collected *in situ* presented here.

Interference among the relatively closely packed sclerites on hash surfaces may have hindered their potential for realignment by currents. Nevertheless, bioclasts on hash Surface 1 show a weak preferred alignment in the NE to SE quadrant; isolated complete cephalia on hash Surface 2 show a preferred orientation to the SW quadrant, although this preference is less clear when all sclerites are considered; and isolated complete cephalia on hash Surface 3 show a preferred orientation to the ESE, with weak trends also to the NNW and SW, although no trend is apparent when all bioclasts are considered (Fig. 15).

6.7. Bioclast dorso-ventral attitude

It has been experimentally demonstrated that complete, isolated cephalia and cranidia adopt a hydrodynamically stable dorsal-up (convex-up) attitude when subjected to surface currents; in the absence of such currents, isolated cephalia settle in an inverted (convex-down) attitude (Hesselbo, 1987; Speyer, 1987, 1991; Mikulic, 1990; Lask, 1993). The dorso-ventral attitude of these sclerites can therefore offer biostratigraphic insight (Speyer and Brett, 1986; Schumacher and Shrike, 1997; Hickerson, 1997), with the caveat

that any current-induced signal can be subsequently modified by surface scavenging (which results in predominantly convex-down sclerite attitudes; Speyer and Brett, 1986; Speyer, 1987) and extensive bioturbation (which may result in random sclerite attitudes, including perpendicular or oblique to the sediment surface; Speyer, 1987). Olenelloid cephalia, which lack facial sutures (contra Speyer, 1987, p. 210), may have hydrodynamic properties similar to the complete cephalia modeled by Lask (1993).

The vast majority of isolated, complete cephalia throughout all well-sampled portions of the succession are preserved in a dorsal-up attitude (Table 6). The lowest proportions (all nevertheless >75%) are found within field unit D and on hash Surfaces 1 and 3.

Different sclerites can have markedly different hydrodynamic properties (Hesselbo, 1987), although these have received less experimental study. In all Ruin Wash strata from which articulated cephalothoraces were recovered, the majority of such specimens were preserved in a dorsal-up attitude (Table 6). However, in intervals from which more than one cephalothorax was recovered (field units C and D) the proportion preserved in a dorsal-up attitude is lower than the proportion of co-occurring complete, isolated cephalia preserved dorsal-up (Table 6), although sample size is low and this difference may not be significant. The clustered cephalothoraces of uncertain stratigraphic provenance (see above) are typically biased in dorso-ventral attitude (Fig. 2a, b), although whether they were predominantly dorsal-up or inverted cannot be determined on these weathered, isolated slabs. The hydrodynamic properties of fragmented cephalia have never been studied. In all carefully sampled portions of the Ruin Wash succession, the proportion of such broken cephalia preserved in a dorsal-up attitude is consistently lower than the proportion of co-occurring complete cephalia preserved dorsal-up, and sometimes <50% (Table 6), although sample size is low in most field units.

6.8. Bioclast fragmentation

As for disarticulation (above), fragmentation of a sclerite may arise through exposure to physical (e.g., turbulence or current action) or biological (e.g., scavenging or predation) processes (Fortey, 1975; Brezinski, 1986; Speyer, 1987, 1991; Speyer and Brett, 1988; Brandt, 1989; Hughes, 1993; Kidwell and Flessa, 1996; Pratt, 1998; Babcock, 2003). Recognizing which of these agents was responsible for the breakage of any particular bioclast is in most cases difficult (Babcock, 2003; see below). [Bioclast fracturing resulting from post-burial sediment compaction is more easily recognized (fragments separated by cracks remain adjacent, for example) and is excluded from consideration here.] Although this compromises the uncritical use of fragmentation data as a simple indicator of environmental energy, transportation distance, or scavenging/predation intensity, such data can still provide useful biostratigraphic information: the frequency of bioclast fragmentation might be expected to inversely correlate with burial rate, for example, because slow sediment accumulation rate increases exposure time of bioclasts to physical and biological agents of breakage.

The present section deals only with fragmentation data for isolated cephalia and for isolated thoracic segments collected from known horizons within the “taphonomy trench”. A detailed discussion of the palaeoenvironmental and palaeobiological implications of bioclast fragmentation at the Ruin Wash Lagerstätte, utilizing a much larger data set (including specimens collected out of precise stratigraphic context), will be presented elsewhere.

The proportion of isolated cephalia and of isolated thoracic segments which have suffered pre-burial fragmentation is stratigraphically non-uniform, and the patterns exhibited by the two sclerite types are remarkably similar (Table 7, Fig. 11). The frequency of sclerite breakage on hash surfaces is typically high (for cephalia, 10%, 25%, and 46% on Surfaces 1, 2 and 3, respectively; for thoracic segments, 100%, 100%, and 98%) relative to that for sclerites recovered from other

intervals. The proportion of broken sclerites within field units B through E progressively declines (for cephalons, 33%, 20%, 8%, and 0%, respectively; for isolated thoracic segments, 85%, 79%, 50%, and 0%).

7. Inferred depositional environment

The sedimentological, microstratigraphical, ichnological, and biostratigraphic data presented above can be used to infer the details of the depositional environment of the Ruin Wash Lagerstätte.

The fine grain size of Ruin Wash sediments, the lack of extensive size-sorting of bioclasts, and the absence of sedimentary structures in field units C through H indicate sediment accumulation in an offshore, low-energy environment, below storm wave base (Speyer and Brett, 1985; see also below). Although it is difficult to conclusively establish a mode of deposition for exclusively fine-grained sediments, several lines of evidence indicate that individual claystone beds were deposited as “event beds”, with fine-grained sediments deposited rapidly as a series of obtrusion events (Brett et al., 1997). This is supported by the preferential

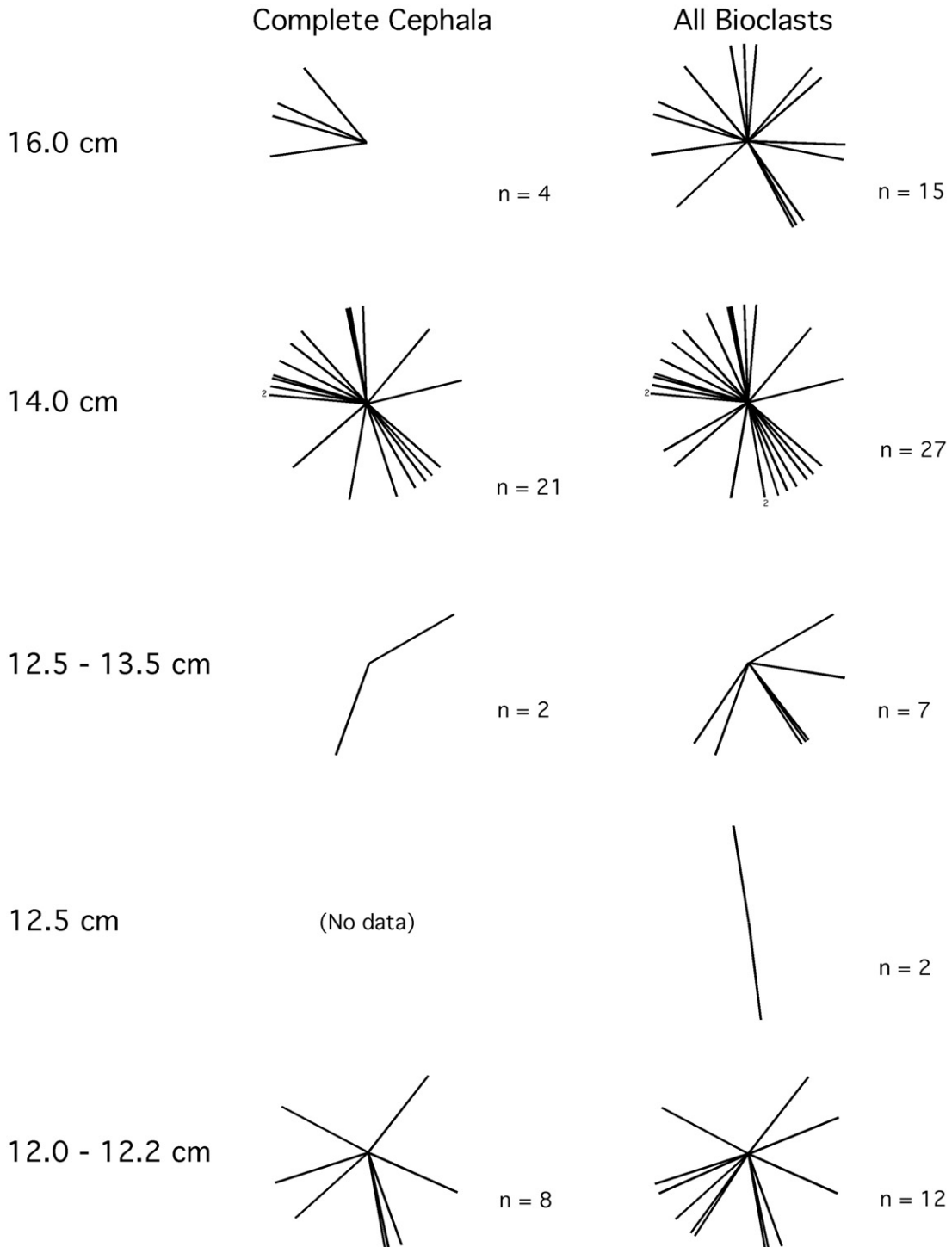


Fig. 16. Orientation (relative to present-day north) of isolated, complete cephalons (left column) and all bioclasts (right column) through several finer subdivisions of field unit C of the Ruin Wash Lagerstätte (see Fig. 4). Small numbers specify number of specimens represented by a vector (not specified when n=1). See text for details.

Table 6
Dorso-ventral attitude of bioclasts through units of the Ruin Wash Lagerstätte

			Unit B	Unit C	Unit D	Surface 1	Unit E	Surface 2	Surface 3
Isolated cephalo	Complete	Total	12	59	35	23	21	34	32
		Dorsal-up	11	55	27	20	19	33	27
		% Dorsal-up	91.67	93.22	77.14	86.96	90.48	97.06	84.38
	Fragmented	Total	6	15	3	5	0	14	63
		Dorsal-up	5	7	2	4	n/a	11	46
		% Dorsal-up	83.33	46.67	66.67	80.00	n/a	78.57	73.02
Articulated remains	Total	0	7	8	1	1	0	0	
	Dorsal-up	n/a	5	5	1	1	n/a	n/a	
	% Dorsal-up	n/a	71.43	62.50	100.00	100.00	n/a	n/a	

occurrence of bioclasts, hash surfaces, and carcasses at the bases of beds, the presence of ichnofabrics developed from the top surfaces of beds downwards, by rare scour features and silt-clay size grading observed within field unit B, and by pervasive, randomly orientated clay microfabrics. Random orientation of clay particles in mudstones is characteristic of flocculated clays deposited from gravity flows in events, whereas claystones accumulated through pelagic or hemipelagic deposition are characterized by a strongly preferred orientation (O'Brien et al., 1980). While extensive bioturbation may also result in randomly orientated clay fabrics (e.g., O'Brien and Slatt, 1990), all parts of the Ruin Wash section, including well bioturbated (i.i. 4), weakly bioturbated (i.i. 2) and non-bioturbated (i.i. 1) depositional beds exhibit randomly orientated clay fabrics, indicating that the clay fabrics are primary, and did not result from secondary disturbance. Given the evidence for rapid deposition and the paucity of silt found within this section, Ruin Wash sediments are consistent with deposition from distal tempestites. These depositional events must have been set up by storm wave disturbance of a muddy shelf environment lying above storm wave base and subsequent downslope flow of the mud under the influence of gravity. During deposition of this succession, the Ruin Wash locality lay far enough removed from source areas subject to storm wave disturbance that the majority of coarse clastic sediments were deposited from suspension prior to reaching Ruin Wash. However, the locality was proximal enough to source areas that sedimentation was event-driven rather than pelagic. This depositional configuration resulted in rapid burial of trilobite remains in the absence of currents capable of significant transport or disturbance of bioclasts, although winnowing of fine-grained sediments and concentration of sclerites seems to have occurred in parts of the section where depositional energy was greatest.

Rapid sedimentation resulting in obrution deposits is also associated with trilobite Lagerstätten in the Middle and Upper Ordovician (Hughes and Cooper, 1999; Karim and Westrop, 2002; Hunda et al., 2006) and in the Devonian (Speyer and Brett, 1985, 1986, 1988, 1991; Brett and Baird, 1986, 1993; Babcock and Speyer, 1987; Speyer, 1987, 1988, 1991; Brett et al., 1997; Hickerson, 1997). Storm-related deposition by gravity currents in the shelf sea is often inferred as a mode of deposition for such event beds, as interpreted here. The Ruin Wash event beds are analogous to the dysaerobic, mud-supported shell beds ("taphofacies model V") recognized by Speyer and Brett (1991) in the Middle Devonian Hamilton Group.

Table 7
Fragmentation of bioclasts through units of the Ruin Wash Lagerstätte

		Unit B	Unit C	Unit D	Surface 1	Unit E	Surface 2	Surface 3
Isolated cephalo	Total	18	74	38	28	21	48	95
	Complete	12	59	35	23	21	34	32
	Fragmented	6	15	3	3	0	12	44
	Uncertain	0	0	0	2	0	2	19
	% Broken	33.33	20.27	7.89	10.71	0.00	25.00	46.32
Isolated thoracic segments	Total	20	29	16	7	1	34	46
	Complete	3	6	8	0	1	0	1
	Fragmented	17	23	8	7	0	34	45
	% Broken	85.00	79.31	50.00	100.00	0.00	100.00	97.83

Specimens exhibiting only compaction-related fracturing are excluded.

Conversely, the hash surfaces are interpreted as simple autochthonous or parautochthonous shell beds (Brett and Baird, 1993; Brett et al., 1997) representing hiatus intervals of either non-deposition or winnowing away of fine-grained siliciclastic sediment, as indicated by the high concentration of skeletal material on hash surfaces relative to the intervening beds. The (weak) preferred orientation of bioclasts on hash Surfaces 1, 2, and 3 indicates slight alignment by low-energy, unidirectional currents, suggesting that sediment winnowing caused hash surface formation when bottom-flowing current energy was sufficient to remove rather than deposit mud. If so, then hash surfaces are analogous to the current-winnowed shell beds ("taphofacies model II") rather than sediment-starved shell beds ("taphofacies model IV") of Speyer and Brett (1991). Development of a hash surface may be parsimoniously interpreted as genetically related to deposition of the overlying event bed: an individual storm-generated sediment flow can first winnow and then deposit sediment as its energy dissipates. The uneven stratigraphic distribution of hash surfaces reflects changes in the perceived intensity of storm-generated currents at the Ruin Wash locality (see also below): the abundance of amalgamated hash surfaces within field units A and I suggests frequent exposure to both the winnowing and depositional phases of storm-generated sediment flow, whereas the scarcity of hash surfaces within field units B to E suggests a relative deepening to below the reach of all but the strongest storm-generated currents such that the winnowing phase was rarely experienced. Alternatively, the amalgamation of hash surfaces within field units A and I is consistent with relative siliciclastic sediment starvation (bypassing) and the stacking of storm layers during this interval. The bioclast association on a winnowed and/or sediment-starved hash surface represents a "within-habitat time-averaged assemblage" of Kidwell and Bosence (1991), defined as an assemblage which accumulated gradually (over an interval of decades to tens of thousands of years; Kidwell, 1993) within a particular environment. There is no evidence that hash surfaces represent lag accumulations with significant erosional truncation (Brett and Baird, 1993), or that any portion of the Ruin Wash succession represents an environmentally condensed sample (more than one environment condensed into a single sample; Kidwell and Bosence, 1991).

The general positive association between the abundance of hash surfaces and the presence of carbonate nodules (Fig. 4) suggests that

growth of carbonate nodules may be linked to the presence of hash surfaces. Speculatively, carbonate nodule growth within the substrate may have been favoured at a particular depth below the sediment–water interface; the prolonged intervals of sediment winnowing (or non-deposition) responsible for development of hash surfaces may have sustained nodule growth at this depth (see Brett et al., 2006 for an example of early diagenetic cementation in muds underlying hash surfaces; also Peters, 2007).

The presence of a minor silt-size grain fraction in field units A and B along with rare scour structures at the bases of beds, and the absence of such features from field units C through G, indicates that obrution events responsible for deposition of the beds in units A and B were more energetic than those depositing beds in the overlying units. Individual beds in units A and B are also typically thicker than beds in overlying units. These data suggest that the event beds in units A and B represent more proximal tempestites (i.e., greater current velocity, higher density sediment cloud, coarser grain size), and those in units C through E represent more distal tempestites. Biostratigraphic data and the sequence stratigraphic architecture (see below) favour interpretation of these changes in the proximality of tempestite deposits in terms of change in relative sea level (deepening-to-shallowing cycle, with maximal flooding coinciding with deposition of unit D and/or E) rather than change in the actual intensity of the storms. Similarly, the scarcity of hash surfaces in units B through E relative to units A and F through I is most parsimoniously interpreted in terms of shifts in relative water depth (above): currents of sufficient strength to induce sediment winnowing occurred less frequently in relatively deeper water.

The extensive bioturbation in field units A and B indicates that oxygen levels were sufficient to permit extensive shallow infaunal colonization and sediment mixing. The lower ichnofabric index and generally tiny size of burrows in beds of field units C through H indicate a subsequent decline in (and occasional preclusion of) infaunal activity (see also interpretation of bioclast dorso-ventral attitude data, below), suggesting benthic oxygen stress (e.g., Savrda et al., 1984). The inferred prevalence of pyrite (now weathered to haematite or limonite–haematite) as burrow infillings and as discrete accumulations within these units also indicates a transition into low oxygen conditions within the substrate (i.e., a very shallow redox boundary). The presence of multiple, relatively thin, event beds within these units reduces the likelihood that infaunal activity was limited solely by rapid sequential deposition of thick piles of sediment. Given the evidence for the autochthonous nature of the relatively diverse benthic epifaunal community (see below), however, favourable conditions apparently prevailed (at least episodically) at and above the sediment–water interface during this interval. Benthic oxygen levels during deposition of the youngest strata (uppermost field unit H and field unit I) apparently returned to levels similar to those experienced during deposition of field units A and B, coincident with an increase in infaunal activity and cessation of pyrite formation. Bottom water oxygen content at Ruin Wash was likely inversely coupled to bathymetry, as inferred depositional energy is inversely correlated with ichnofabric index.

Preservation of bioclasts within tempestites raises the obvious concern as to whether (and by how much) the bioclasts were transported into the final burial site by storm-induced gravity currents. This is particularly important when making palaeoecological inferences regarding the preserved biota. Studies of modern depositional environments demonstrate that significant transportation of individuals out of their life habitat is rare and can typically be easily recognized (Westrop, 1986; Kidwell and Flessa, 1996). There is no convincing evidence of significant transportation of the Ruin Wash trilobite fauna. In terms of its taxonomic composition, the trilobite fauna is neither unique to this locality nor foreign relative to surrounding localities, and is therefore unlikely to be allochthonous on a regional scale (Brett and Baird, 1993). The similarity of species relative abundances in all units and on all surfaces suggests that taxon

occurrence was not differentially biased among strata (e.g., by taxon-specific sclerite sorting): within-habitat bioclast sorting (Speyer, 1983; Westrop, 1986) was absent or at least uniform across taxa throughout the succession.

Hydrodynamically sorted or current-aligned specimens would indicate at least local transport (Fortey, 1975; Brett and Baird, 1993). However, the wide size range of specimens preserved on single surfaces and within single units suggests that size-sorting, and by inference current transportation, of the assemblage was minimal (Fortey, 1975; Brandt, 1989). It is likely that bottom currents (perhaps associated with event bed deposition, above) did wash away the tiniest and/or most lightweight sclerites, given the under-representation of pygidia, hypostomes and thoracic segments in the field samples, and given that the scarcity of small (<2 mm) cephalae in the Ruin Wash claystones seems not to stem from collecting bias (above). However, the fact that sclerites as small as 1 to 3 mm were preserved suggests that such bottom currents were very weak and/or only sporadically developed.

There is evidence for weak current-alignment of (some) bioclasts within field unit B (in agreement with sedimentary structures), portions of unit C, and unit E, but not within unit D. Presumably this weak realignment of bioclasts occurred during event bed deposition. The weakness or absence of a preferred orientation within any unit could be attributed to either low current velocity or to lack of consistency in current direction (individual event beds are analytically time-averaged into units, above). The lack of substantial size-sorting (above), the lack of current-induced sedimentary structures above the basal 12 cm of the succession, and the presence of fragile but non-disrupted exuviae (see below) favours low current velocity as the likely explanation. However, the direction of the possible preferred orientation (when present) does differ among units (see above), suggesting that lack of consistency in current direction may also have been a factor.

The preservation of most trilobite bioclasts in a dorsal-up attitude may indicate that they were either (1) subject to unidirectional currents and adopted a hydrodynamically stable disposition; or (2) rapidly buried prior to inversion by physical or biological disturbance (because the dorsal-up attitude was also the life attitude and that resulting from normal exuviation in olenelloids). Independent evidence for low current velocity (above) favours the latter hypothesis, at least for bioclasts on non-winnowed (i.e., non-hash) surfaces.

The preservation of articulated exoskeletons, particularly intact exuviae, is usually taken to imply minimal disturbance (e.g., by transportation, scavenging, or bioturbation) prior to rapid burial (Fortey, 1975; Brezinski, 1986; Brett and Baird, 1986, 1993; Speyer, 1985, 1987, 1991; Speyer and Brett, 1986, 1988; Brandt, 1989; Hughes, 1993). Arthropod carcasses can actually withstand considerable transportation without disarticulation (Allison, 1986; Babcock and Chang, 1997; Babcock et al., 2000). However, moult ensembles are highly likely to disarticulate as a result of transportation, and the preservation of intact trilobite exuviae offers a reliable indication of autochthoneity (Fortey, 1975; Speyer and Brett, 1985; Brett and Baird, 1986, 1993; Speyer, 1987; Mikulic, 1990; Brett and Allison, 1998; Gaines and Droser, 2003; Brett et al., 2006; Paterson et al., 2007). Disarticulation can also occur without environmental or ecological disturbance, as a result of decay-related gas release from a carcass prior to burial (Brett and Baird, 1986; Speyer and Brett, 1988). Studies on modern arthropods have shown that disarticulation occurs within hours to weeks after death or ecdysis (Schäfer, 1972; Plotnick, 1984, 1986; Allison, 1986, 1988; Speyer, 1987; Plotnick et al., 1988; Brett and Baird, 1986, 1993; Briggs and Kear, 1994; Babcock and Chang, 1997; Babcock et al., 2000), and trilobites are assumed to have followed a similar decay rate.

Given that trilobite sclerites of differing hydrodynamic character have been shown to segregate by current action (references listed above), the preservation of disarticulated sclerites of the same individual (e.g., cephalon slightly displaced from thorax; Fig. 2c) in close spatial

proximity, plus the co-occurrence of isolated cephalons, isolated thoracic segments, and articulated remains (carcasses and exuviae; Fig. 2e, f), all of a wide range of sizes, suggests minimal transportation and rapid burial of the Ruin Wash fauna within the clay beds of field units B through E.

Articulated material is rare to absent on hash surfaces, as would be expected given the prolonged exposure time and/or stronger current activity on these winnowed planes. The increasing proportion of articulated specimens in field units B through D and the subsequent decline in field unit E suggests that turbulence and/or pre-burial exposure time progressively decreased up-section, reaching a minimum in unit D, and then progressively increased from unit E to the top of the succession. The lack of a convincing preferred orientation of bioclasts within unit D (see above) also agrees with this inference. These data are consistent with the hypothesis of relative deepening of the shelf sea during deposition of units B through D, then relative shallowing during deposition of unit E. The increased bed thickness, the greater abundance of hash surfaces, the coarser maximum grain size, the extent of substrate oxygenation and infaunal activity, the presence of scour features in units A and B, and the greater abundance of hash surfaces in units F through I, are all consistent with extrapolations of this deepening-to-shallowing trend to the base and to the top of the Ruin Wash succession, respectively.

Event beds such as distal tempestites provide a means for the *in situ* preservation of minimally disturbed trilobite remains. Deposition of each event bed would have been rapid, resulting in smothering and burial of the benthic community (living individuals, exuviae, and partially or completely disarticulated sclerites lying on the seafloor) below the taphonomically active zone (Davies et al., 1989). Preservation of prone, intact carcasses (Fig. 2e) with no signs of escape response suggests that living individuals were killed and buried by the obrution event (Speyer and Brett, 1985, 1988; Brezinski, 1986; Hughes and Cooper, 1999). The fauna preserved within each event bed represents a minimally time-averaged, single-event concentration or census assemblage (Kidwell and Bosence, 1991; Brett and Baird, 1993; Brett et al., 1997; Hunda et al., 2006), although it may include some reworked bioclasts attaining final burial. Elsewhere in the marine fossil record such assemblages are typically time-averaged over just days to hundreds of years (Kidwell, 1993; Behrensmeyer et al., 2000); this provides an estimate of the absolute magnitude of time-averaging within each event bed.

Fragmentation data provide one final source for inference of exposure time. The high frequency of bioclast breakage on hash surfaces is consistent with the interpretation of these surfaces as winnowed or hiatal planes with extended pre-burial exposure time and/or subjection to more intense current activity. The relatively lower frequency of bioclast breakage within field units B through E is consistent with rapid burial by event beds and consequent decreased exposure time and/or subjection to intense current action. The declining frequency of damage in field units B through D is consistent with the inferred increase in water depth at the locality (above). However, these other lines of evidence suggest that maximal water depth and lowest intensity of disturbance was attained during deposition of unit D; fragmentation data indicate that the lowest incidence of bioclast damage occurs within unit E. Inference as to potential agents of bioclast breakage are discussed at length elsewhere.

Although only known from slabs collected from the Lagerstätte but out of precise stratigraphic context, clusters of articulated cephalothoraces (e.g., Fig. 2a, b) represent spectacular associations of bioclasts with unusual preservational qualities. Each spatially restricted cluster consists predominantly of large, articulated exoskeletons showing preferred orientation(s) and a bias in dorso-ventral attitude, albeit of unknown polarity (see above). The virtual absence of small bioclasts and the common orientation of the exoskeletons could be taken to indicate that cluster-bearing surfaces were subject to relatively strong water currents. (If so, then the bias in dorso-ventral attitude should be in favour of dorsal-up individuals.) However,

currents strong enough to induce such marked size-sorting of bioclasts would be expected to also winnow away the fine-grained sediment (resulting in formation of a hash surface), and perhaps to have brought in silt-sized grains. Neither of these predictions is met on the available cluster-bearing slabs, and a purely mechanical explanation for the clusters is deemed unlikely. Rather, we interpret the clusters to represent the fortuitous burial of live or recently dead individuals by an obrution event of energy sufficient to cause bioclast realignment but insufficient to cause sediment winnowing. Under this interpretation, the clusters represent minimally time-averaged, simple smothered-bottom communities. For any individuals alive at the time of burial, death (presumably by suffocation) must have been rapid given the failure of such large individuals to exhume themselves from the relatively thin sediment blanket. The scarcity of small individuals within the clusters likely represents behavioural or ecological segregation rather than physical sorting; conceivably this segregation was related to the prevailing oxygen conditions at the seafloor, which periodically reached dysoxic levels during deposition of field units C through G and presumably induced oxygen stress among the trilobite benthos. The dysaerobic benthic conditions may have been sufficient to permit colonization of the seafloor by (large) trilobites, but promoted rapid oxygen depletion from the porewaters of freshly deposited entombing fine-grained sediments. The oxygen-limited conditions would have inhibited scavenging and bioturbation (to the extent that these were developed during the Dyeran), promoting intact preservation of the fauna by subsequent tempestite deposition (see also Peters, 2007). Such a scenario is consistent with the available microstratigraphic and biostratigraphic data, and suggests that the environmental conditions responsible for the formation and preservation of the clusters (i.e., rapid burial of a minimally time-averaged community by the distal products of a tempestite) were subtly different than those responsible for the formation and preservation of hash surfaces (i.e., sediment winnowing then deposition under the influence of a more proximal tempestite, forming then burying a more extensively reworked, time-averaged, assemblage).

Babcock (2003, pp. 74–75) interpreted such “monospecific clusters” of *Olenellus gilberti* and of *Olenellus chiefensis* at Ruin Wash in terms of burial preserving reproductive behaviour in those species. The large number of specimens within a cluster was deemed suggestive of a high reproductive rate. The lack of “obvious predation-resistant structures such as large spines” was considered a further indication of reliance on a high rate of reproduction as a reproductive strategy in these trilobites (Babcock, 2003, p. 74). However, all Ruin Wash trilobite clusters examined by the present authors are polytaxic (e.g., Fig. 2a, b) and all Ruin Wash olenelloid species possess large spines (genal spines, macropleural third thoracic segment, axial spine on the fifteenth) which surely deterred predation to some extent. The taxa involved in clusters vary among slabs (e.g., *O. gilberti* clustered with *O. chiefensis* on some slabs but with *Olenellus fowleri* on others), refuting potential interpretation of polytaxic clusters in terms of sexual dimorphs grouped for reproduction. Furthermore, it is unclear why occurrence in clusters would necessarily relate to a high reproductive rate. Although strong cases for reproductive clustering of trilobites have been made (see Paterson et al., 2007 for a Cambrian example), a hypothesis involving size-related segregation in response to prevailing benthic (oxygen) conditions or, more speculatively, in response to predation seems better supported for the Ruin Wash clusters.

8. Summary

The 43 cm Ruin Wash Lagerstätte succession is interpreted as a stacked series of event beds (tempestites), deposited by events progressively waning in perceived intensity (i.e., represented by increasingly distal tempestites) from the base of the section through to the middle of the succession (field unit D or E), then progressively waxing in perceived intensity (i.e., represented by increasingly more

proximal tempestites) to the top of the succession. The perceived intensity of the events recorded at Ruin Wash was likely a function of overlying water depth (eustatic sea level), which progressively increased then decreased through the interval; an alternative mechanistic hypothesis of cyclicity in storm intensity is plausible but less in keeping with biostratigraphic data and sequence stratigraphic architecture. More turbulent, proximal tempestite depositional events winnowed away sediment from the seafloor, resulting in the concentration of bioclasts on time-averaged hash surfaces, prior to depositing sediment. The turbulence associated with event bed deposition was sufficient to transport away the smallest and most lightweight sclerites (especially hypostomes and isolated thoracic segments), but insufficient to cause dramatic reorientation of the remaining bioclasts or disruption of articulated trilobite remains (including delicate exuviae). Bottom water oxygen concentrations appear to have varied inversely with water depth (and positively with depositional energy). The Lagerstätte records a series of autochthonous, smothered-bottom communities and more extensively time-averaged hash surfaces, all preserved by obrution events.

The whole succession was deposited in a moderately deep water setting, below storm wave base. Similar trilobite Lagerstätten of the Upper Ordovician and Middle Devonian were estimated to have accumulated 20–100 m below sea level (Schumacher and Shrike, 1997, and references therein; see also Brett et al., 2006); this bathymetric range seems reasonable for the Ruin Wash site. The late Dyeran was a time of general sea level rise during which large-scale carbonate production ceased in this region of the Laurentian Cordilleran margin. The Ruin Wash Lagerstätte was deposited during a higher-order deepening-to-shallowing cycle superimposed on this general transgression; the final such cycle recognized within the traditional “Lower Cambrian” of Laurentia. The lower two-thirds (field units A through E) of the Lagerstätte represent an early transgressive to peak highstand systems tract. Single-event concentration (census assemblage; smothered-bottom) trilobite Lagerstätten are often associated with the large accommodation space, low-energy, basal portions of a parasequence (Brett et al., 1997, 2006; Hunda et al., 2006). It remains to be seen whether high-resolution sequence stratigraphy can be used as a predictive tool for the discovery of new trilobite and/or soft-tissue preservation Lagerstätten.

Marked taphonomic bias in the abundance, composition, size, and fragmentation of trilobite remains within the monofacial succession at Ruin Wash resulted from environmental shifts so subtle as to leave no distinct lithological signature. Here we have shown that integration of detailed microstratigraphic, ichnologic, and biostratigraphic data allows the recognition of such cryptic shifts in palaeoenvironment (see also Brett and Allison, 1998). Such an approach permits identification and removal of taphonomic bias from the fossil record, and may be crucial for the accurate reconstruction of palaeocommunity composition and structure.

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