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A new hypothesis for organic preservation of Burgess Shale taxa in the middle Cambrian Wheeler Formation, House Range, Utah

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Abstract

Cambrian *konservat-lagerstätten* are the most significant fossil deposits for our understanding of the initiation of Phanerozoic life. Although many modes of preservation may occur, these deposits most frequently contain nonmineralized fossils preserved in the form of kerogenized carbon films, a rare yet important taphonomic pathway that has not previously been explained for any unit by a comprehensive model. The middle Cambrian Wheeler Formation of Utah, one of these *lagerstätten*, contains abundant kerogenized preservation of nonmineralized tissues, which occurs within a distinctive taphofacies that accumulated under the following conditions: (1) domination of the siliciclastic fraction by clay-sized particles, (2) close proximity to a carbonate platform, which resulted in mixed carbonate-clay sediments, (3) a well-developed oxygen minimum precluding benthic colonization and burrowing, and (4) relative proximity to oxic bottom-waters, facilitating transport of organisms from a habitable environment to one that favored their preservation. We propose that preservation of nonmineralized tissues in the Wheeler Formation may have resulted from a combination of influences that reduced permeability and, thus, lowered oxidant flux, which in turn may have restricted microbial decomposition of some nonmineralized tissues. Those influences include near bottom anoxia, preventing sediment irrigation by restriction of bioturbation; reducing conditions near the sediment–water interface that may have acted to deflocculate aggregations of clay minerals, resulting in low permeability face-to-face contacts; early diagenetic pore occluding carbonate cements; and an absence of coarse grains such as silt, skeletonized microfossils, fecal pellets, or bioclasts. This model may be applicable to kerogenized preservation of macrofossils in other fossil *lagerstätten*.

Keywords: Cambrian; *Lagerstätten*; Wheeler Formation; Burgess Shale; Taphonomy; Diagenesis

1. Introduction

Fossilization of nonmineralized tissues provides unparalleled anatomical and ecological information (Allison and Briggs, 1991). The celebrated fauna of

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the Burgess Shale contains more than 40 genera of nonmineralizing organisms, which were distributed globally during early and middle Cambrian time (Conway Morris, 1989). Although very uncommon, Cambrian deposits bearing preservation of nonmineralized tissues are more abundant than those of any other geologic period, even when normalized for outcrop area and time (Allison and Briggs, 1993a). Cambrian nonmineralized fossils are preserved in many taphonomic modes, the most significant of which is "Burgess Shale-type preservation", defined by Butterfield (1995) as the fossilization of nonmineralizing organisms as kerogenized organic carbon films under fully marine conditions. While spectacular examples of preservation via mineralization of originally non-biomineralized tissues are known from Cambrian deposits (e.g., Briggs and Nedin, 1997), Burgess Shale-type preservation is the most common mode of nonmineralized tissue preservation in lower and middle Cambrian *lagerstätten* worldwide (Butterfield, 1990). Despite considerable inquiry into the depositional environments of these deposits (e.g., Allison and Brett, 1995; Babcock et al., 2001), the conditions that promoted Burgess Shale-type preservation remain poorly understood. In this paper, we investigate the circumstances of this important taphonomic pathway in the middle Cambrian Wheeler Formation of Utah.

Anoxia is frequently invoked as a causal agent in preservation of nonmineralized tissues. However, although it is strongly correlated with preservation of nonmineralized tissues, anoxia alone does not inhibit decomposition (e.g., Allison, 1988; Butterfield, 1990, 1995). Efforts to understand other physical factors that may have been, in part, responsible for the abundance of preservation of nonmineralized tissues in the Cambrian have focused on two related aspects of the problem: specific taphonomic pathways that led to the preservation of nonmineralized fossils, and the secular trend in preservation of nonmineralized tissues over the Phanerozoic. Butterfield (1995) argued that secular variation in dominant clay mineralogy resulted in temporal optima for the stabilization of organic material through absorption of decay-inducing enzymes onto the surfaces of particularly reactive clay minerals. In this view, the early and middle Cambrian represented a fortuitous preservational window when conditions favoring nonmineralized fossil preservation were maximized. This idea was not supported by a metamorphic study of the Burgess Shale (Powell, 2003), which found that the original clay mineralogy of the Burgess Shale was neither unusual nor rich in highly reactive clay minerals. Wollanke and Zimmerle (1990) also noted a correlation between preservation of nonmineralized tissues and clay-rich, fine-grained sediments, and suggested that burial in such sediments was an important prerequisite for preservation of nonmineralized tissues. A recent conceptual model (Petrovich, 2001) suggested that under "sub-oxic" conditions, Fe^{2+} bound to the surfaces of chitin and other organic biopolymers, inhibiting the ability of bacterial enzymes. These hypotheses are difficult to test with available physical evidence.

The most commonly cited hypothesis addressing the secular trend suggests that the likelihood of preservation of nonmineralized tissues was greatest before the advent of bioturbation in muddy substrates, implying that Burgess Shale and like faunas were "burrowed away" from the fossil record (Allison and Briggs, 1993a,b). The advent of significant bioturbation would have had a profound impact upon basic physical properties and early diagenetic processes in marine sediments, and has been held responsible for a number of secular changes including increased nutrient cycling (McIlroy and Logan, 1999) the taphonomic loss of Ediacaran biotas (Gehling, 1999), and the loss of thin event beds from the rock record, coincident with the development of the mixed layer (Droser et al., 2002). In a field test of the "burrowed away" hypothesis, Allison and Brett (1995) found that preservation of nonmineralized tissues and discrete trace fossils in the Burgess Shale were confined to mutually exclusive horizons, and concluded that bioturbation, as regulated by bottom-water oxygen content, was responsible for inhibiting preservation of nonmineralized tissues.

In this paper, we develop an alternative, permeability-based taphonomic model for preservation of nonmineralized tissues of organic-walled macrofossils in the middle Cambrian Wheeler Formation. The Wheeler Formation of the House Range, Millard County, Utah (39°N, 113°W), is one of several Cambrian deposits traditionally considered *konservat-lagerstätten* (Conway Morris, 1998) and provides an excellent opportunity to address these questions.

2. Geological setting

Middle Cambrian strata in the House Range and vicinity (Fig. 1) were deposited in what has been interpreted as a fault-controlled trough, termed the House Range Embayment (Fig. 2; Rees, 1986). Here, a geographically abrupt change in lithofacies juxtaposes platform carbonates found north and south of the embayment with fine-grained terrigenous and carbonate deposits within the embayment. The lowest-energy deposits within the embayment, which include the Wheeler Formation, are characterized by a dominance of well-laminated strata, the presence of pyrite, and paucity of shelly benthic faunas, reflecting deposition in an oxygen-deficient environment (Rees, 1986). Wheeler Formation-age deposits in the House Range embayment occur across much of Western Utah (Fig. 2), and are well known for dramatic lateral facies changes, including those that occur within the House Range (Rees, 1986). For this reason, a number of formation names have been applied (Rees, 1986). Units to which the name “Wheeler Shale” or “Wheeler Formation” have been applied include a variety of carbonate and mixed carbonate-siliciclastic lithofacies representing deposition in basinal, deep ramp, and shallow ramp deposits (Rees, 1986). In this study we have focused on well-known basinal localities in the Wheeler Amphitheater region of the House Range. In these sections of Wheeler Formation, sediment was derived from two sources: terrigenous mud delivered to the basin during times of increased continental runoff; and carbonate mud, most likely derived from the adjacent platform. Typical Wheeler mudstone is dominated by clay-sized terrigenous material

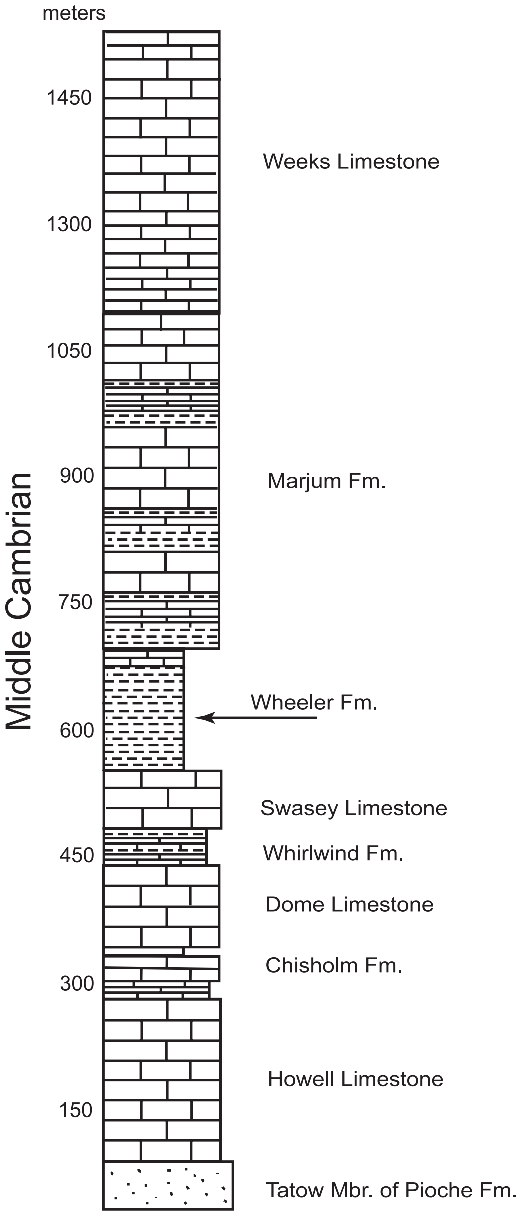


Fig. 1. Middle Cambrian stratigraphy of the House Range, after Hintze and Robison (1975).

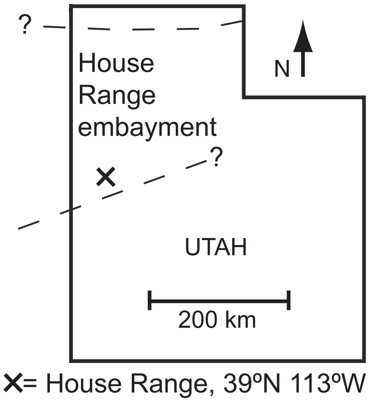


Fig. 2. Location map of the study area, showing the areal extent of the House Range Embayment, as defined by Rees (1986).

Table 1
Weight percent of mineral phases present in six samples from the Wheeler Formation, as determined by Quantitative XRD using the method of Srodon et al. (2001)

	Quartz	Plagioclase	Calcite	Dolomite	2:1 Al clay	2:1 Fe clay	Chlorite	Total clay	Total $CaCO_3$	Total
NTF 1	21	3.2	22.6	0	38.3	0	19	57.3	22.6	104.1
NTF 2	17.3	3.8	36.3	0	19.7	3.3	12.5	35.5	36.3	92.9
NTF 3	14.5	7.2	35.8	0	15.8	0	19.3	35.1	35.8	92.6
ETF 1	22	2.9	26.8	13.2	34.5	0	3.7	38.2	40	103.1
ETF 2	19.7	2.8	12.0	8.5	39.1	0	9.9	49.9	20.5	92.0
ETF 3	19.7	2.3	34.6	3.9	32.0	0	10.6	42.7	38.5	103.1

Samples NTF 1–3 come from the nonmineralized preservation taphofacies; samples ETF 1–2 come from unbioturbated intervals of the *Elrathia* taphofacies; sample ETF 3 comes from a bioturbated interval of the *Elrathia* taphofacies. Totals indicate ≤8% total error in each case.

(<5 μm) with 30–40% detrital micrite and authigenic carbonate (Table 1).

3. Methods

Mudstones commonly are very poorly exposed and appear featureless and massive where found in outcrop. Sedimentary features such as grain-size, bedding, and ichnofabric are rarely observed even in the best outcrops, because they are obscured by weathering, cleavage, fracturing, and the generally small size of primary features. For this reason, 1-to-5-m-thick sections in the Wheeler Formation were continuously sampled in duplicate after thorough outcrop study to capture maximum variation in sedimentologic and taphonomic attributes. Continuous sampling of mudstones is often impossible, but was facilitated in this case by significant carbonate content of Wheeler mudstones and aridity of the study area. One set of samples was slabbed and logged on a millimeter scale. Incorporating thin-section study and X-radiography, logs recorded features of bedding/lamination, ichnology (depth, extent, and style of bioturbation), and early diagenesis, particularly authigenic precipitation of pyrite, calcite, and dolomite. The second set of samples was used for taphonomic and geochemical analyses. Bulk mineralogy was assessed using X-ray diffraction, and weight percent carbonate was determined by coulometric analysis. Quantitative X-ray diffraction also was performed on selected samples using the method of Srodon et al. (2001). In this method, a zinc oxide standard with known peak intensity is mixed with the sample for analysis to determine weight percent of dominant minerals using integrated peak intensities. Composition of organic fossils was determined using energy dispersive X-ray spectroscopy (EDX) on points selected using a scanning electron microscope. For this analysis, samples were coated with platinum and analyzed with a 5-kV beam in order to avoid penetration of the beam into the matrix underlying the thin fossil. Stable carbon isotopic ratios of authigenic and whole-rock carbonate were analyzed online after digestion with 100% phosphoric acid and are reported relative to PDB.

4. Results

4.1. Nature and composition of Wheeler Formation sediments

Sedimentary features, grain-size, and carbonate/clay ratios of mudstones were highly consistent in all sections examined. With the exception of very rare (aeolian) quartz silt grains (<1%) and authigenic crystals, only fine-grained clay and micrite particles are present. Within each taphofacies, mudstones consist of 1-to-12-mm-thick couplets with gray bases grading into black tops. Grain-size changes within couplets are not apparent in thin-section (although rare grading occurs). Couplets are dominated by thin continuous laminae. Cut and fill, ripples, and convolute bedding are absent, indicating that deposition occurred dominantly from suspension with little current reworking. Fecal pellets, clay aggregates, or wavy laminae are not present, arguing against a pelagic biogenic or microbial mat origin. Skeletonized microfossils are also absent. Fluorescent-light microscopy indicates that most laminae contain aggregates of micron-sized blocky calcite crystals which are morphologically consistent with microbially mediated calcite peloids described by Chafetz (1986) as common constituents of marine carbonate rocks; these indicate a detrital origin for carbonate. Authigenic carbonate cements are the most prominent feature of Wheeler mudstone fabric (Fig. 3) and occur as abundant dispersed, micron-sized crystals, as cone-in-cone calcite coatings on the ventral sides of trilobite carapaces, and in thin (<1 mm) continuous horizons.

Quantitative X-ray diffraction indicates the prominent mineral phases are calcite (both micrite and authigenic), quartz, illite, chlorite, and minor plagioclase (in order of abundance; Table 1). During burial diagenesis, the original clay mineralogy was most likely altered to form the current illite, chlorite, quartz, and feldspar assemblage.

Cathodoluminescence indicates that carbonate diagenesis appears to have been restricted to a single early phase of authigenic carbonate cementation. Thin sections show uniform orange luminescence of authigenic carbonates under cathodoluminescent light, whereas authigenic carbonates formed in multiple phases most commonly show distinctive luminescent color banding under cathodoluminescent light. The cements show no evidence of recrystallization sub-

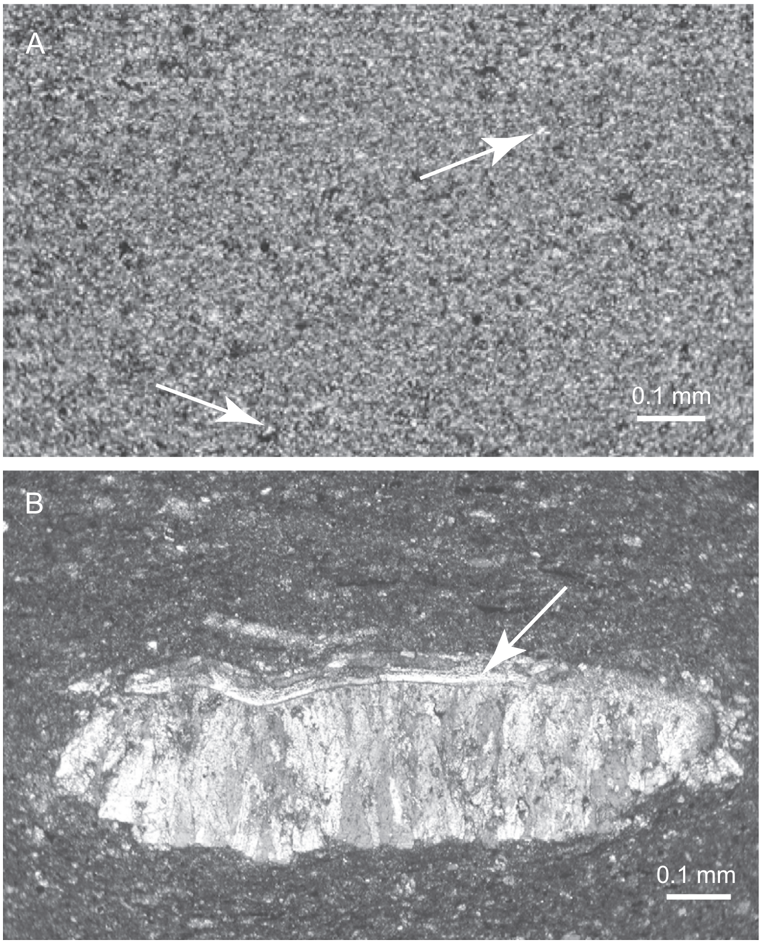


Fig. 3. Polarized-light photomicrographs from the nonmineralized preservation taphofacies (A) and *Elrathia* taphofacies (B). In each, minute authigenic carbonate grains, which appear as bright spots, dominate the mudstone fabric; examples are indicated by arrows in A. B additionally shows a recrystallized trilobite carapace (indicated by arrow) with cone-in-cone calcite cement coating the ventral side, and more prominent authigenic carbonate grains dispersed throughout the fabric.

sequent to emplacement. Deformation of sedimentary laminae around cement-lined trilobite nodules indicates cementation prior to burial compaction. Additionally, the presence of authigenic calcite with the absence of authigenic dolomite in one taphofacies (Table 1) is noteworthy; the significance of this is discussed below. δ^{13}C values from carbonate phases of whole-rock samples vary between -1.65‰ and -0.43‰ PDB (n=14) and are similar to authigenic phases: -0.47‰ to -0.31‰ PDB (n=4). All values fall within the range of δ^{13}C seawater values reported for this time interval of -2‰ to $+0.4$‰ (Montañez et al., 2000).

Despite considerable continuity in sedimentary structures and bulk chemistry, mudstone sections examined exhibit considerable variation in body fossil content, presence/absence of in situ benthic faunas, ichnofabric, and taphonomic features. In this paper, we describe two taphofacies within basinal Wheeler mudstones.

4.2. Nonmineralized preservation taphofacies

The unbioturbated nonmineralized preservation taphofacies is the most commonly occurring taphofacies of the Wheeler Formation, and it is dominant in the lower portion of the unit. This taphofacies contains abundant nonmineralized preservation of the macroscopic, non-calcified algae *Marpolia spissa* (Fig. 4), *Yuknessia simplex*, *Margaretia dorus* and *Morania fragmenta*, as well as unidentifiable worms, likely priapulids. Other nonmineralized taxa which were found to occur rarely in this taphofacies include the priapulid *Selkirkia*, the sponge *Choia*, and undetermined phyllocarid arthropods. Additionally, at least 21 other genera of nonmineralized metazoa, dominantly arthropods, which were not recovered in this study, are known from the Wheeler Formation, most of which are common to the Burgess Shale (Robison, 1991). Nonmineralized fossils are uniformly black and reflective in appearance. Energy dispersive X-ray spectroscopy of representative samples revealed that these fossils are composed of carbon in the form of thin, two-dimensional films (Fig. 5). Nonmineralized taxa are found in association with abundant agnostid trilobites, presumably pelagic in life habit (Robison, 1972; Müller and Walossek, 1987), and rare examples of the “ptychopariid” trilobite *Elrathia kingii*.

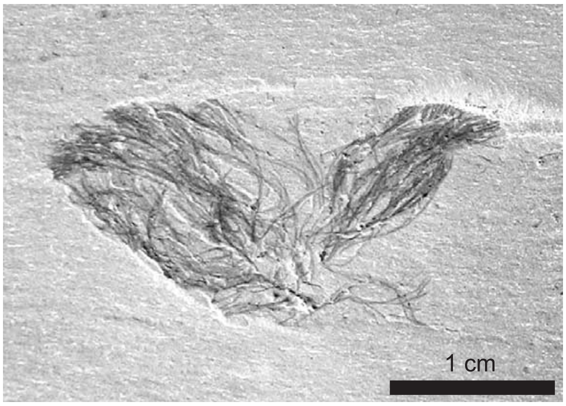


Fig. 4. Burgess Shale-type preservation of the non-calcified alga *Marpolia spissa* from the Wheeler Formation.

Examination of cut slabs as well as thin sections indicates that the nonmineralized preservation taphofacies is characterized by a near-total lack of bioturbation (Fig. 6A). Very rare burrows are horizontal, commonly pyritized, and confined to individual bedding planes. Authigenic pyrite is found within local aggregations dispersed throughout the sediment as well as within burrows. Thin-section analysis reveals the common presence of micron-sized euhedral calcite crystals dispersed through the sediment. Calcite crystals also line the ventral side of agnostid trilobite carapaces, imparting a three-dimensional relief uncommon to trilobite fossils in mudstones. Dolomite is notably absent from this taphofacies (Table 1).

The absence of bioturbation and limited presence of authigenic pyrite suggest that the nonmineralized preservation taphofacies accumulated under dominantly anoxic conditions that excluded a benthic fauna. Rare discrete, horizontal burrows were likely emplaced during short-lived variations in dissolved oxygen concentration. Algae and priapulid worms, which are interpreted to have been infaunal (Conway Morris, 1998), represent an allochthonous fauna, as do rare occurrences of *Elrathia*. Agnostid trilobites inhabited overlying oxic waters, supplying molts and carcasses to the basin below. Rare in situ occurrences of nonmineralized faunas (e.g., the sponge *Choia*) occur on single bedding planes, and are interpreted to represent a “taphonomic window”. In these cases, ichnologic evidence indicates that these single-horizon blooms occur at the transition from

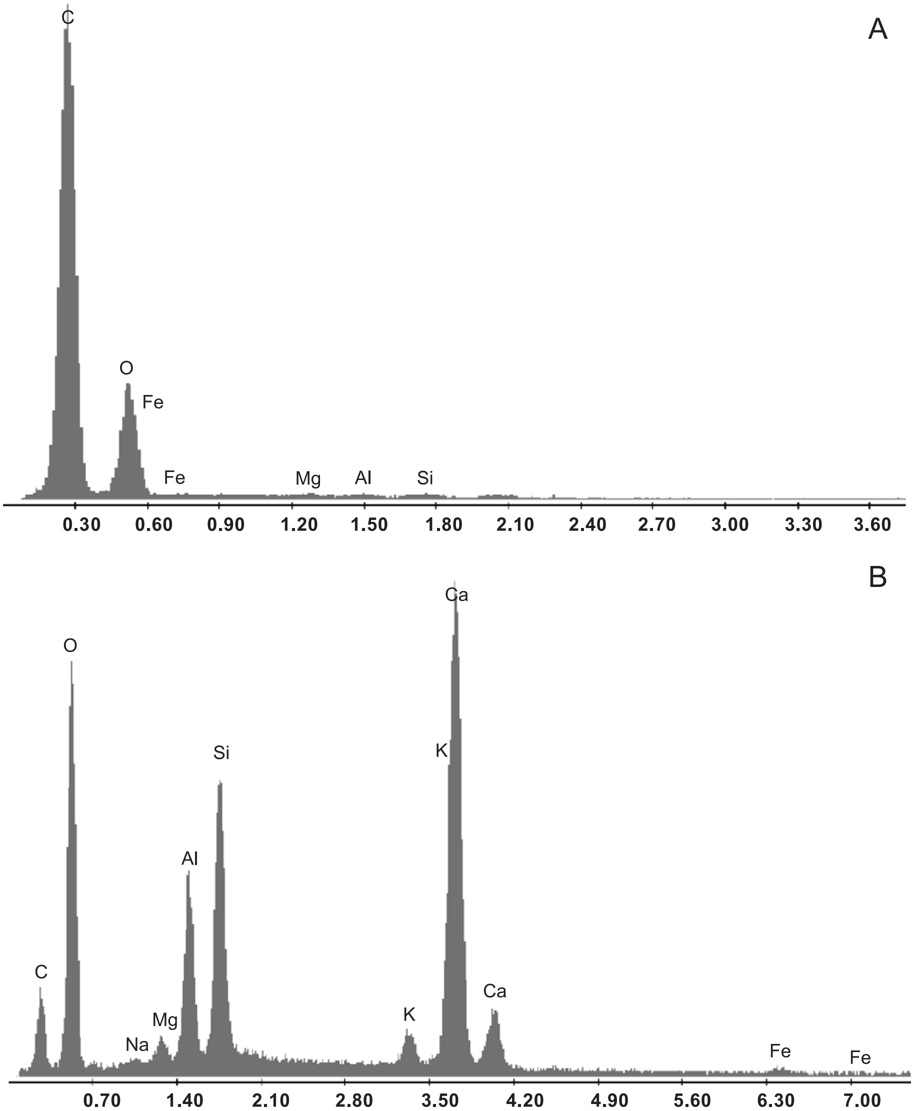
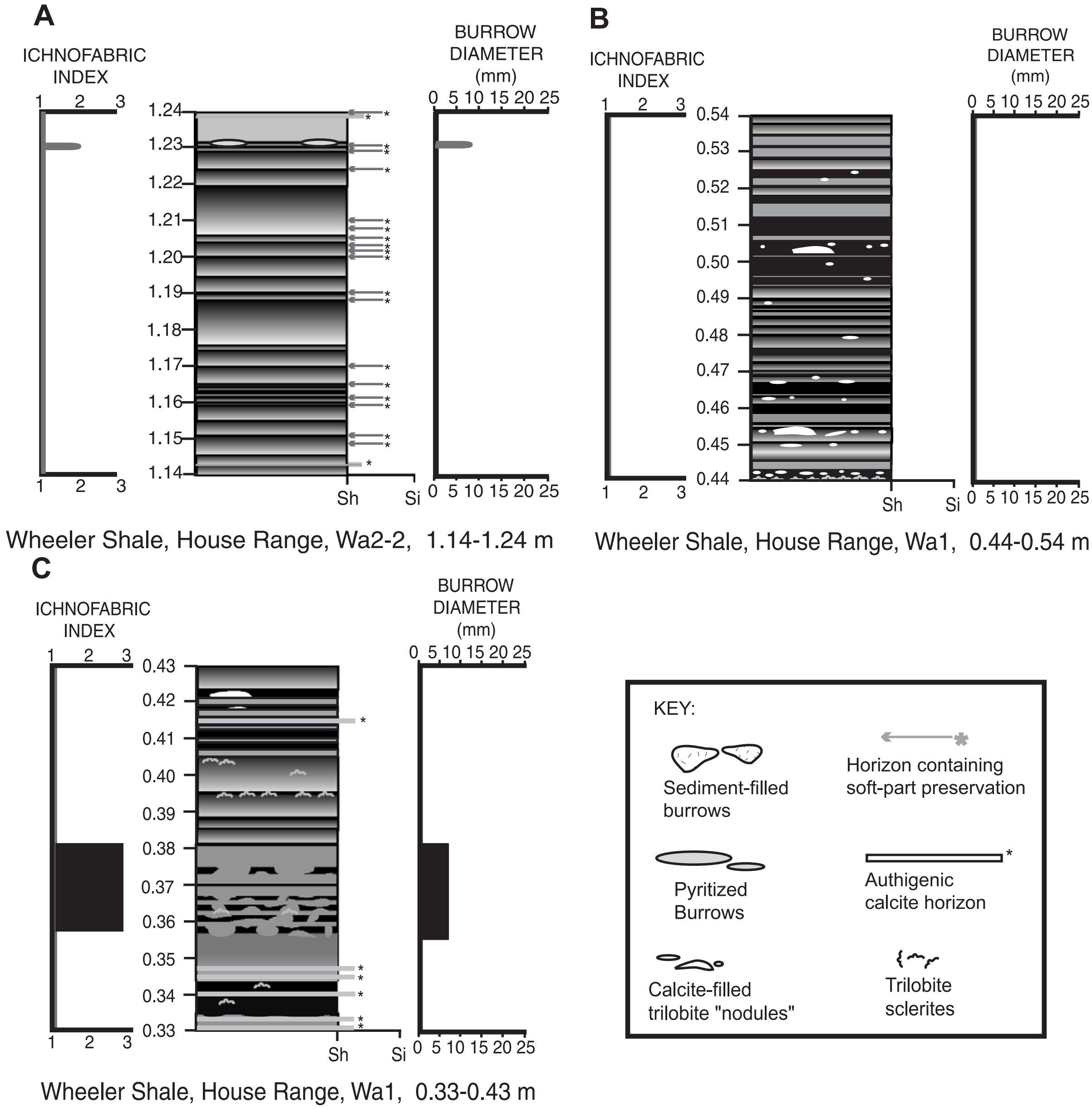


Fig. 5. Energy dispersive X-ray spectra for an organic-walled vermiform metazoan (A) and adjacent matrix of the same specimen (B), using 5-kV beam. Note dominance of carbon in fossil (A) vs. aluminosilicate and carbonate composition of matrix (B).

weakly bioturbated to laminated strata, indicating that short-lived habitable bottom-water conditions facilitated limited benthic colonization, but were followed by an abrupt shift to anoxic conditions, which encouraged preservation (see Discussion).

4.3. *Elrathia taphofacies*

The *Elrathia* taphofacies contains bioturbation in some horizons, and is the dominant taphofacies of the upper part of the Wheeler Formation. It is characterized by unusually abundant *Elrathia kingii* trilobites, preserved as nodules with the recrystallized exoskeleton forming a cap from which 0.5–3-mm calcite crystals radiate outward, from the ventral side only. *Elrathia kingii* is found in association with several species of other ptychopariid trilobites, which occur rarely, common agnostid trilobites, and rare algae and acrotretid brachiopods. Algae constitute the only preservation of nonmineralized tissues observed in this taphofacies.



Wheeler Shale, House Range, Wa2-2, 1.14-1.24 m

Wheeler Shale, House Range, Wa1, 0.44-0.54 m

Wheeler Shale, House Range, Wa1, 0.33-0.43 m

Fig. 6. (A) Detailed log of 10-cm interval within the nonmineralized preservation taphofacies. (B and C) Detailed logs of two 10-cm intervals within the *Elrathia* taphofacies, illustrating non-bioturbated (B) and bioturbated (C) intervals.

Although dominantly unbioturbated (i.i. 1) (Fig. 6B), 2-to-10-cm-thick bioturbated horizons are present (i.i. 2–3; Fig. 6C), separated by 15-to-30-cm-thick intervals of unbioturbated strata (i.i.1). Bioturbated intervals contain subhorizontal to vertical discrete burrows (10 mm max. depth) including *Hormosiroidea* and/or indistinct mottling of mudstone fabric. Authigenic pyrite occurs dispersed throughout the sediment and in local aggregations. The shale fabric of the *Elrathia* taphofacies contains dispersed authigenic calcite and up to 13.2% (by weight) dolomite.

Low levels of bioturbation in many horizons suggest that limited oxygenation of bottom-waters facilitated colonization of the seafloor by a benthic fauna, including *Elrathia*, but precluded significant infaunal activity. Taphonomic, size-frequency, and orientation data indicate that *Elrathia* present are in situ even in unbioturbated intervals, suggesting at least minimal availability of bottom-water oxygen throughout the entire taphofacies. Gradational increases in bioturbation suggest oscillations in bottom-water oxygen content that regulated benthic activity. The restriction of dolomite to this taphofacies may imply a seawater source of Mg^{+2} during diagenesis not present in the nonmineralized preservation taphofacies. We interpret the presence of dolomite in this taphofacies to reflect more efficient pore–water exchange with bottom-waters, and/or more complete organic diagenesis than in the nonmineralized preservation taphofacies (see Discussion below).

5. Discussion

Any attempt to assign a causative mechanism to preservation of nonmineralized tissues in the Wheeler Formation must address the following observations: (1) Nonmineralized fossils occur in laminated strata with no vertical bioturbation and rare horizontal bioturbation, while bioturbation is common in other lithologically similar facies. (2) Nonmineralized fossils are housed in homogenous, clay-rich sediments containing abundant detrital and authigenic carbonate, and lacking in silt, fecal pellets and skeletonized microfossils. (3) Taphofacies are sedimentologically and mineralogically similar, and are composed of laminated suspension deposits. (4) Nonmineralized fossils are preserved as organic carbon films and are not replaced, mineralized, or preserved as molds.

The most significant difference between the nonmineralized preservation taphofacies and the *Elrathia* taphofacies lies in the record of bioturbation and implied relative bottom-water oxygen content. This, however, does not provide an adequate explanation for preservation of nonmineralized tissues. Oxidation rates of many organic compounds are comparable under anoxic (given unlimited SO_4^{2-}) or oxic conditions (Henrichs and Reeburgh, 1987; Lee, 1992). Additionally, laboratory experiments have shown rapid and complete decomposition of crustaceans buried in muddy sediments under anoxic conditions (Allison, 1988). Limited exposure to all oxidants (including SO_4^{2-}) is likely a more critical factor than the relatively minor metabolic efficiencies of one oxidant over another.

Still, preservation of nonmineralized tissues in the Wheeler Formation shows a strong correlation with bottom-water anoxia. We interpret this relation to be the indirect result of oxygen's influence on a primary control of preservation of nonmineralized tissues, permeability, which ultimately controls total oxidant exposure. Oxygen influences permeability in two distinct ways. First, anoxia reduces burrowing and the associated irrigation effects (Savrda et al., 1984). Burrowing directly disturbs only a limited amount of organic matter in the sediment, but churning and disruption of sediments promote a deeper redox boundary and open pathways enhancing pore–water exchange of oxidants, which sustain microbial decomposition of organic matter (Aller, 1982).

Second, anoxic conditions near the sediment–water interface may reduce permeability in clay-rich suspension deposits by deflocculating clays, allowing low permeability face-to-face contact of clay platelets (Moon and Hurst, 1984). Clay floccules (face-to-edge contacts forming aggregates) increase porosity and promote greater pore–water exchange. Under reducing conditions in low turbulence environments, organic cations common in anoxic water such as amino and humic acids, coat charged clay surfaces, and may break surface-to-edge contacts and allow aggregates to disperse (Moon and Hurst, 1984). Laminated microfabrics formed by suspension settling of clay particles, such as that of the Wheeler Formation, have the lowest permeability of fine-grained sediments (Davies et al., 1991). The intervals of the Wheeler Formation bearing nonmineralized fossils are comprised of this laminated microfabric and do not contain fecal pellets, silt, mineralized microfossils, or other particles that otherwise might enhance permeability. Biogenic particles, especially agnostid trilobite sclerites, are present here, but are volumetrically insufficient to impact permeability. Differences in bottom-water oxygen content resulted in important permeability differences between the two taphofacies described here, as it restricted bioturbation, and also may have facilitated deflocculation of clay aggregates in the nonmineralized preservation taphofacies.

Further reduction of permeability, limiting oxidant exchange with seawater also was driven by pore-occluding carbonate cementation. Carbonate cementation is common in early diagenetic environments (Coleman, 1985) and is driven by sulfate reduction or dissolution and reprecipitation of highly reactive high-Mg calcite mineralogies typical of the extremely fine-grained micritic aggregates that comprise the detrital carbonate phase in the Wheeler. Evidence that carbonate cementation was early and derived predominantly from the detrital phase includes abundant dispersed authigenic carbonate, detrital-like carbon isotope values in authigenic cement, and evidence for early cementation from calcite-lined trilobite carapaces. δ^{13}C values from carbonate phases in the Wheeler Formation support a detrital marine or marine origin of carbonate phases, rather than an origin from organic diagenesis. Although organic diagenesis leads to the production of alkalinity, driving carbonate precipitation (e.g., Mazzullo, 2000), several authors have pointed to the importance of a precursor detrital carbonate phase in the genesis of authigenic carbonates (Baker and Burns, 1985; Compton, 1988; Mazzullo, 2000; Mullins et al., 1985; Irwin, 1980). Sulfate reduction and coincident pyrite precipitation commonly lead to carbonate dissolution and subsequent re-precipitation (Coleman, 1985). Whole-rock values from the Wheeler Formation vary between -1.65‰ and -0.43‰ PDB (n=14). Authigenic phases range from -0.47‰ to -0.31‰ PDB (n=4). Uniformly, these values lie within the range of δ^{13}C seawater values reported for this time interval of -2‰ to $+0.4$‰ (Montañez et al., 2000). Any contribution from organic diagenesis must have been minor, as carbon derived as a result of these processes would have driven carbonate values toward lower δ^{13}C. The minor presence of authigenic pyrite, however, indicates that limited sulfate reduction occurred at some stage of diagenesis. Therefore, authigenic carbonate cements in the Wheeler Formation appear to have been derived from the dissolution and re-precipitation of a portion of the reactive detrital micrite phase.

Low exchange of porewater with seawater and/or arrested organic diagenesis in intervals bearing preservation of nonmineralized tissues is suggested by the absence of dolomite as an authigenic phase in the nonmineralized preservation taphofacies, whereas dolomite is a significant component (up to 13.2% by weight) of the sedimentologically identical and interbedded *Elrathia* taphofacies. Precipitation of dolomite implies a seawater source of Mg^{+2}, and, thus, may indicate seawater–porewater exchange in the Elrathia taphofacies that did not occur in the nonmineralized preservation taphofacies. Alternately, if sufficient Mg^{+2} to form dolomite was present in porewaters initially, dolomite absence from the nonmineralized preservation taphofacies may indicate incomplete sulfate reduction during carbonate cementation, since the presence of SO_4^{2-} may inhibit dolomite formation (Baker and Kastner, 1981). Since authigenic dolomite typically forms only after sulfate reduction is complete (Coleman, 1985), dolomite absence from the nonmineralized preservation taphofacies would additionally imply an early cessation of organic diagenesis in this taphofacies, likely through occlusion of porosity. Ongoing work will test these possibilities through isotopic analysis of sulfur to determine if the early diagenetic systems were open or closed to sea water sulfate.

The combined effects of low original porosity, the porosity-reducing effects of anoxia, and early carbonate cementation may have resulted in porosity occlusion to an extent sufficient to restrict microbial activity and, thus, to facilitate Burgess Shale-type preservation in the Wheeler Formation (Fig. 7). Original low porosity was facilitated by the inboard sequestration of all but the finest clastics and also by the absence of fecal pellets and skeletonized microfossils. Skeletonized microfossils are not significant components of Cambrian sediments in general (Tucker, 1974), and the oldest known microfossil oozes do not occur until the late Cambrian (Tolmacheva et al., 2001). Within fine-grained sediments, the abundance of skeletonized microfossils is positively correlated with porosity and also with size of individual pore spaces (Kraemer et al., 2000). Therefore, the subsequent rise to abundance of skeletonized microfossils in marine sediments and likely increase in the abundance of fecal pellets may be important porosity-influencing secular trends.

The hypothesis that a post-middle Cambrian increase in bioturbation may be responsible for the observed secular decline in preservation of nonmineralized tissues is not entirely supported in the

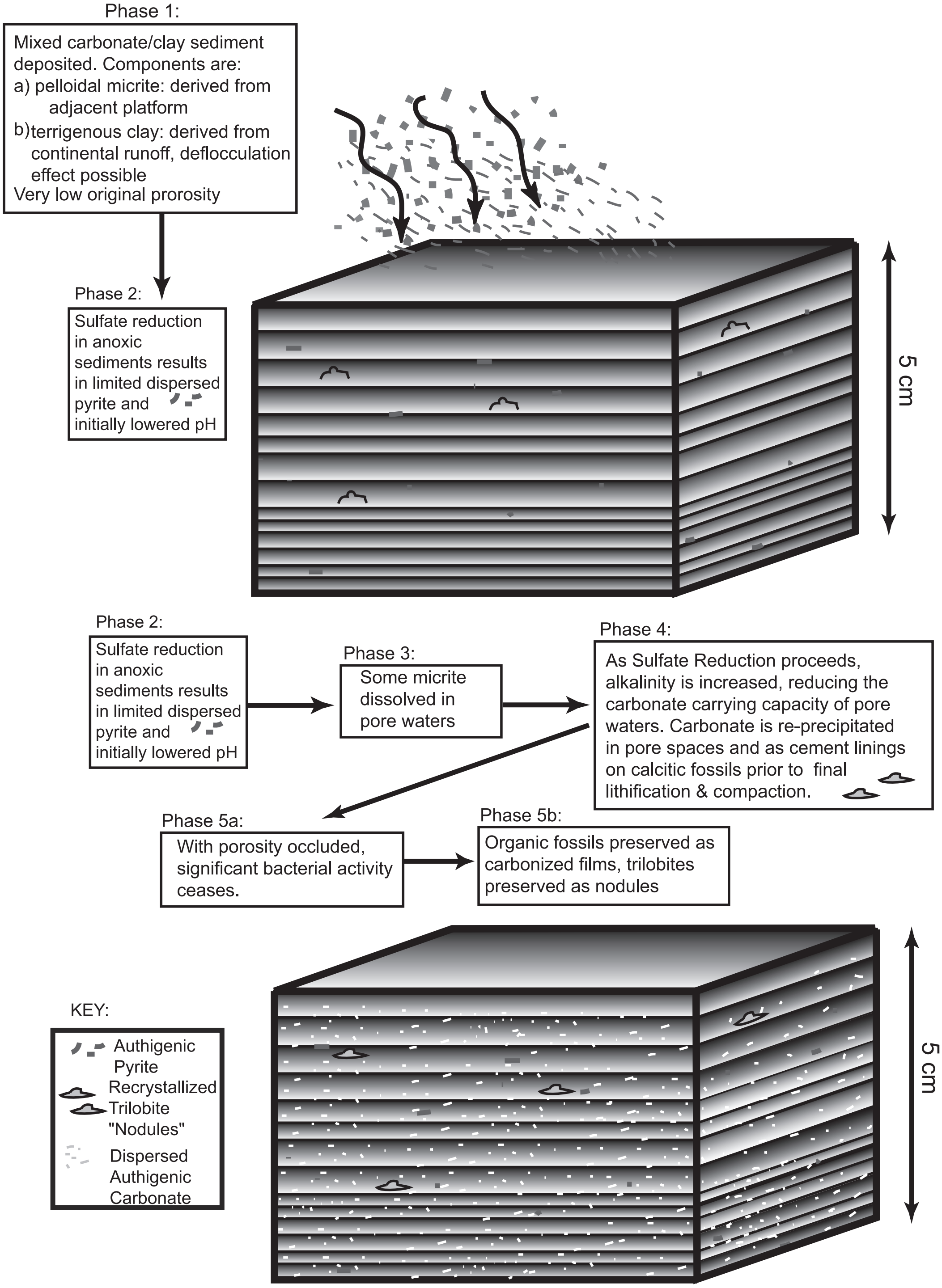


Fig. 7. Schematic summary of porosity-occlusion model, showing early diagenetic processes proposed to have promoted Burgess Shale-type preservation in the nonmineralized preservation taphofacies of the Wheeler Formation. Trilobites shown in this summary are pelagic agnostids, however calcite coatings on the ventral sides of *Elrathia* found in the *Elrathia* taphofacies were emplaced via the same processes.

Wheeler Formation, as bioturbation was already established in this environment to an extent sufficient to limit preservation of nonmineralized tissues, but was regulated by bottom-water oxygen content. A subsequent increase in maximum depth of bioturbation (Droser and Bottjer, 1988) also would have had little effect on the preservation potential of nonmineralized tissues in the most basinal environments of the Wheeler Formation, as bioturbators were excluded for meters of preserved continuous section. Within the nonmineralized preservation taphofacies, however, strata deposited closer to the anoxic–dysoxic boundary may be interbedded at a decimeter scale with mudstones deposited under more oxic conditions, and commonly contain low levels of shallow-tier bioturbation, as also observed in the lower Cambrian Latham Shale (Gaines and Droser, 2002). Preservation of nonmineralized tissues in these more marginal expressions of the nonmineralized preservation taphofacies, which often contain the most metazoan fossils, would almost certainly have been jeopardized by a subsequent increase in maximum depth of bioturbation.

The early porosity closure scenario of exceptional preservation is also applicable to two other Great Basin *lagerstätten*, the Marjum Formation and the “shallow Wheeler” *lagerstätte* of the Drum Mountains (Robison, 1991), which are exclusively fine-grained, carbonate-rich, possess the same prominent diagenetic fabrics, and contain trilobites preserved in the same unusual taphonomic mode. These formations share a common depositional environment and submarine paleogeography proximal to a carbonate platform and, thus, may be considered expressions of the same facies. The Burgess Shale and other Cambrian *lagerstätten* of Laurentia also occur near the shelf break/carbonate platform edge (Conway Morris, 1998), and may represent additional expressions of this taphofacies. These deposits would provide a useful test of this hypothesis. Physical mechanisms proposed by Butterfield (1995) and Petrovich (2001) for further stabilization of organic matter are not inconsistent with our porosity closure model and may be important contributing factors for the stabilization of organic tissues at a finer scale. This facies was lost from late Cambrian cratonic deposits of the Great Basin with the widespread progradation of carbonate platforms. If minimal porosity is indeed important to the organic preservation of nonmineralized tissues, secular trends in the type and quantity of biogenic contributions to sediments may provide an interesting comparison with the secular decline in Burgess Shale-type preservation.

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References

Aller, R.C., 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall, P.L., Tevesz, M.J.S. (Eds.), Animal–Sediment Relations, the Biogenic Alteration of Sediments. Plenum Press, New York, pp. 53–96.

Allison, P.A., 1988. The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. Paleobiology 14, 139–154.

Allison, P.A., Brett, C.E., 1995. In situ benthos and paleo-oxygenation in the middle Cambrian Burgess Shale, British Columbia, Canada. Geology 23, 1079–1082.

Allison, P.A., Briggs, D.E.G. (Eds.), 1991. Taphonomy: Releasing the Data Locked in the Fossil Record. Plenum Press, New York, pp. 25–90.

Allison, P.A., Briggs, D.E.G., 1993a. Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. Geology 21, 527–530.

Allison, P.A., Briggs, D.E.G., 1993b. Burgess Shale biotas: burrowed away? Lethaia 26, 184–185.

Babcock, L.E., Zhang, W., Leslie, S.A., 2001. The Chengjiang biota; record of the early Cambrian diversification of life and clues to exceptional preservation of fossils. GSA Today 11, 4–9.

Baker, P.A., Burns, S.J., 1985. Occurrence and formation of dolomite in organic-rich continental margin sediments. AAPG Bull. 69, 1917–1930.

Baker, P.A., Kastner, M., 1981. Constraints on the formation of sedimentary dolomite. Science 213, 213–215.

Briggs, D.E.G., Nedin, C., 1997. The taphonomy and affinities of the problematic fossil *Myoscolex* from the Lower Cambrian Emu Bay Shale of South Australia. J. Paleontol. 71, 22–32.

Butterfield, N.J., 1990. Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. Paleobiology 16, 272–286.

Butterfield, N.J., 1995. Secular distribution of Burgess Shale-type preservation. Lethaia 28, 1–13.

Chafetz, H.S., 1986. Marine peloids: a product of bacterially induced precipitation of calcite. J. Sediment. Petrol. 56, 812–817.

Coleman, M.L., 1985. Geochemistry of diagenetic non-silicate minerals: kinetic considerations. Philos. Trans. R. Soc. Lond., A 315, 39–56.

Compton, J.S., 1988. Degree of supersaturation and precipitation of organogenic dolomite. Geology 16, 318–321.

Conway Morris, S., 1989. The persistence of Burgess Shale-type faunas: implications for the evolution of deeper-water faunas. Trans. R. Soc. Edinb. Earth Sci. 80, 271–283.

Conway Morris, S., 1998. The Crucible of Creation. Oxford University Press, Oxford. 242 pp.

Davies, K.D., Bryant, W.R., Vessell, R.K., Burkett, P.J., 1991. Porosity, permeabilities and microfabrics of Devonian shales. In: Bennett, R.H., Bryant, W.R., Hulbert, M.H. (Eds.), Microstructure of Fine-grained Sediments. Springer Verlag, New York, pp. 109–119.

Droser, M.L., Bottjer, D.J., 1988. Trends in depth and extent of bioturbation in Cambrian carbonate marine environments, western United States. Geology 16, 233–236.

Droser, M.L., Jensen, S., Gehling, J.G., 2002. Trace fossils and substrates of the terminal Proterozoic–Cambrian transition: implications for the record of early bilaterians and sediment mixing. Proc. Natl. Acad. Sci. 99, 12572–12576.

Gaines, R.R., Droser, M.L., 2002. Depositional environments, ichnology, and rare soft-bodied preservation in the lower Cambrian Latham Shale, East Mojave. SEPM Pac. Sect. Book 93, 153–164.

Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. Palaios 14, 40–57.

Henrichs, S.M., Reeburgh, W.S., 1987. Anaerobic mineralization of marine sediment organic matter: rates and the role of anaerobic processes in the oceanic carbon economy. Geomicrobiol. J. 5, 191–237.

Hintze, L.F., Robison, R.A., 1975. Middle Cambrian stratigraphy of the House, Wah Wah, and adjacent ranges in Western Utah. Geol. Soc. Amer. Bull. 86, 881–891.

Irwin, H., 1980. Early diagenetic carbonate precipitation and pore fluid migration in the Kimmeridge Clay of Dorset, England. Sedimentology 27, 577–591.

Kraemer, L.M., Owen, R.M., Dickens, G.R., 2000. Lithology of the upper gas hydrate zone, Blake Outer Ridge: a link between diatoms, porosity, and gas hydrate. Proc. Ocean Drill. Program Sci. Results 164, 229–236.

Lee, C., 1992. Controls on organic carbon preservation: the use of stratified water bodies to compare intrinsic rates of decomposition in oxic and anoxic systems. Geochim. Cosmochim. Acta 56, 3323–3355.

Mazzullo, S.J., 2000. Organogenic dolomitization in peritidal to deep-sea sediments. J. Sediment. Res. 70, 10–23.

McIlroy, D., Logan, G.A., 1999. The impact of bioturbation on infaunal ecology and evolution during the Proterozoic–Cambrian transition. Palaios 14, 58–72.

Montañez, I.P., Osleger, D.A., Banner, J.L., Mack, L.E., Musgrove, M.L., 2000. Evolution of the Sr and C isotope composition of Cambrian oceans. GSA Today 10, 1–7.

Moon, C.F., Hurst, C.W., 1984. Fabric of mud and shales: an overview. In: Stow, D.A.V., Piper, D.J.W. (Eds.), Fine-grained Sediments, Geological Society Special Publication, vol. 15, pp. 579–593.

Müller, K.J., Walossek, D., 1987. Morphology, ontogeny, and life-habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. Fossils Strata 19, 1–124.

Mullins, H.T., Wise Jr., S.W., Land, L.S., Siegel, D.I., Masters, P.M., Hinchey, E.J., Price, K.R., 1985. Authigenic dolomite in Bahamian peri-platform slope sediment. Geology 13, 292–295.

Petrovich, R., 2001. Mechanisms of fossilization of the soft-bodied and lightly armored faunas of the Burgess Shale and of some other classical localities. Am. J. Sci. 3001, 683–726.

Powell, W., 2003. Greenschist-facies metamorphism of the Burgess Shale and its implications for models of fossil formation and preservation. Can. J. Earth Sci. 40, 13–25.

Rees, M.N., 1986. A fault-controlled trough through a carbonate platform: the middle Cambrian House Range embayment. GSA Bull. 97, 1054–1069.

Robison, R.A., 1972. Mode of life of agnostid trilobites: 24th International Geological Congress, Montreal, Canada, Section 7 (Paleontology). pp. 33–40.

Robison, R.A., 1991. Middle Cambrian biotic diversity; examples from four Utah *Lagerstätten*. In: Simonetta, A.M., Conway Morris, S. (Eds.), The Early Evolution of the Metazoa and the Significance of Problematic Taxa. Cambridge University Press, Cambridge, pp. 77–98.

Savrda, C.E., Bottjer, D.J., Gorsline, D.S., 1984. Development of a comprehensive oxygen-deficient marine biofacies model: evidence from Santa Monica, San Pedro, and Santa Barbara Basins, California continental borderland. AAPG Bull. 68, 1179–1192.

Srodon, J., Drits, V.A., McCarty, D.K., Hsieh, J.C.C., Eberl, D.D., 2001. Quantitative X-ray diffraction analysis of clay-bearing rocks from random preparations. Clays Clay Miner. 49, 514–528.

Tolmacheva, T.J., Danelian, T., Popov, L.E., 2001. Evidence for 15 m.y. of continuous deep sea biogenic siliceous sedimentation in early Paleozoic oceans. Geology 29, 755–758.

Tucker, M.E., 1974. Sedimentology of Paleozoic pelagic limestones; the Devonian Griotte (southern France) and Cephalopodenkalk (Germany). Spec. Publ. Int. Assoc. Sedimentol. 1, 71–92.

Wollanke, G., Zimmerle, W., 1990. Petrographic and geochemical aspects of fossil embedding in exceptionally well preserved fossil deposits. Mitt. Geol.-Paläontol. Inst. Univ. Hamb. 69, 57–74.