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# New Approaches to Understanding the Mechanics of Burgess Shale-type Deposits: From the Micron Scale to the Global Picture

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## ABSTRACT

Cambrian Burgess Shale-type (BST) deposits are among the most significant deposits for understanding the “Cambrian explosion” because they contain the fossilized tissues of nonmineralized organisms and provide a substantially different window on the radiation of the Metazoa than is afforded by the more “typical” fossil record of skeletal parts of biomineralized organisms. Despite nearly a century of research, BST deposits remain poorly investigated as sedimentologic entities largely because they comprise fine-grained mudrocks. Here, we describe a new, integrative approach to understanding a single BST deposit, the middle Cambrian Wheeler Formation of Utah, which reveals a dynamic interplay of paleoenvironmental, paleoecologic, and sedimentologic/diagenetic factors within a superficially homogeneous lithofacies. This millimeter-scale microstratigraphic and paleontologic approach is augmented by both outcrop and microscopic study. These types of data are applicable to issues of quite different scales, including micron-scale diagenetic processes involved in fossil preservation, organism-environment interactions and paleoecology of the early Metazoa, and regional and global controls on the distribution of BST deposits.

## BURGESS SHALE-TYPE DEPOSITS: THE GLOBAL PICTURE

Cambrian lagerstätten (Conway Morris, 1989) provide a fortuitous window into one of the most dramatic episodes in evolutionary history. Represented most famously by the Burgess Shale (middle Cambrian of British Columbia), these deposits are noteworthy for two major reasons. First, they provide an excellent record of ancient biodiversity because they contain fossils that are not preserved under normal circumstances. Whereas the “normal” fossil record is almost exclusively a record of hard, mineralized skeletal parts, these deposits preserve some labile, nonmineralized tissues of organisms, including those lacking hard skeletal parts. Secondly, these deposits, which are rare in the geologic record as a whole, are moderately abundant in lower and middle Cambrian strata, an interval spanning the

time of the “Cambrian explosion.” In the rock record, this interval is marked by the relatively sudden appearance of fossils representing most animal phyla, the acquisition of skeletal hard parts by a number of animal groups, and the advent of predation and complex metazoan in ecosystems (e.g., Seilacher, 1997; Zhuravlev and Riding, 2001; Babcock, 2003). In this paper, we present a unified framework for understanding the dynamic interplay of sedimentological, paleoecological, and paleoenvironmental factors that controlled the preservation and distribution of fossils in a single Burgess Shale-type deposit, the Wheeler Formation (middle Cambrian) of western Utah.

## NEW APPROACHES

Many BST deposits, including the Wheeler Formation and the Burgess Shale, represent deposition just offshore of broad carbonate

platforms, at sharp shelf-slope breaks (Conway Morris, 1998; Rees, 1986). Classic models for the Burgess Shale have considered the depositional environment to be fully anoxic, due to the exquisite preservation of fossils, and the dark color of the mudrocks (e.g., Conway Morris, 1986). This implies that the faunas were transported, yet some assemblages of fossils, such as the well-known *Ogygopsis* trilobite beds in the Burgess Shale and horizons that contain delicate sponges, clearly occur in situ. Important questions, key to a first-order understanding the biotas in an ecological sense, have remained: Can discrete, paleoecologically meaningful assemblages be resolved from within the homogeneous sediments? Were bottom water oxygen conditions sufficient to permit episodic, frequent, or sustained benthic colonization by in situ faunas? Because of the extraordinary importance of these biotas, a better knowledge of the relationships of the organisms to the paleoenvironments that they inhabited and/or facilitated their preservation is desirable.

In order to begin to address these interrelated problems, we focused on the middle Cambrian Wheeler Formation of western Utah, which contains abundant Burgess Shale-type preservation of nonmineralized fossils, including common macroscopic algae and a diverse fauna of more than 20 genera of more rarely occurring arthropods, priapulids, sponges, and cnidarians (Robison, 1991). It also contains a well-described and diverse skeletal fauna (Robison, 1964, 1991). The formation is well exposed and readily accessible over a broad area in the House Range (39°15' N, 113°20' W) and immediate vicinity. The study area is arid and also has not been subjected to extensive compressive stress. As a result, mudrocks of the Wheeler Formation are less strongly altered by the effects of tectonics and weathering than are other important BST deposits.

Mudrocks present unique challenges to study. Unlike other types of sedimentary rocks that are more readily interpreted in the field, mudrocks most often appear featureless and massive. Thus, in a stratigraphic context, mudrocks are commonly interpreted to represent static, monotonous conditions, or are occasionally subdivided on the superficial basis of color. Mudrocks comprise the bulk (60%) of the sedimentary record, yet remain poorly understood (Potter et al., 1980). However, recent methodological advances in the study of mudrocks have demonstrated that intensive, fine-scale approaches can yield much information about depositional processes and paleoenvironments (e.g., Schieber 2003). The

suite of depositional environments represented by mudrocks is typically characterized by low-energy deposition, relatively continuous sedimentation, and, often, little current reworking in comparison to coarser-grained deposits. Furthermore, mudrocks often contain *in situ* fossil assemblages, making them particularly good candidates for paleoecological and paleoenvironmental study.

An integrative, millimeter-scale, methodology, incorporating aspects of sedimentology and paleontology was applied. In the field, short (1-5 m) intervals were targeted for intensive study and sampled continuously in duplicate. In the laboratory, these short sections were reconstructed and slabbed parallel to bedding, then etched lightly with dilute HCl to reveal primary and secondary sedimentary features. Using direct analysis of the slabbed samples in combination with thin section study, the sections were logged on a millimeter scale. The duplicate sets of samples were split along bedding planes for paleontological analysis, and the microstratigraphic positions of fossils were incorporated into the logs. These techniques were complemented by compositional (XRD, EDX, coulometry), geochemical ( $\delta^{13}\text{C}$ ;  $\delta^{18}\text{O}$ ), microscopic (SEM, fluorescent light, cathodoluminescent), and imaging (X-ray) analyses.

## PALEOENVIRONMENTS AND BOTTOM-WATER OXYGEN

The Wheeler Formation accumulated in what has been interpreted as a fault-bounded trough, termed the House Range embayment, at the edge of an expansive carbonate platform (Rees, 1986). At most localities, the Wheeler Formation is composed of homogenous, fine-grained mudrocks, with smaller thicknesses of thin-bedded, fine-grained carbonates. Burgess Shale-type biotas occur only in the mudrock facies. Wheeler mudrocks, which represent the lowest energy deposits found in the region, represent deposition in a basin adjacent to the distal end of a carbonate ramp (Rees, 1986). The thin-bedded carbonates and interbedded mudrocks comprising the distal ramp facies of the House Range embayment consist of sub-millimeter-thick micro-graded beds, interpreted to represent down-ramp gravity flows deposited below the influence of storm waves (Elrick and Hinnov, 1996). The basal mudrock facies typically grades upwards into distal ramp deposits. Basal mudrock sediments of the Wheeler Formation are characterized by: 1, exclusively fine grain size (<50 $\mu$ ); 2, mixed carbonate-clay composition (17-47 wt. % carbonate); 3, color-graded gray-black

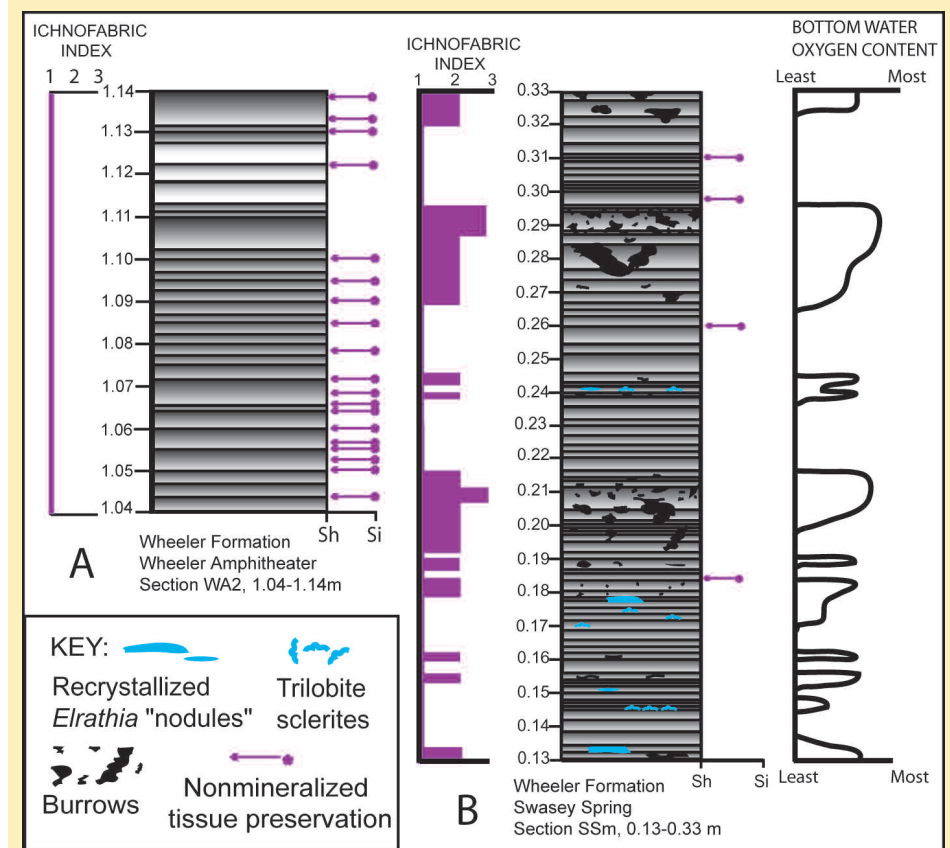


Figure 1. Microstratigraphic logs from the Wheeler Formation illustrating the context of nonmineralized preservation. A. 10-cm interval with complete absence of bioturbation and Burgess Shale-type preservation in most beds, typical of sustained anoxic benthic conditions in the Wheeler Formation. B. 20-cm interval showing cm-scale oscillations in bioturbation, bottom water oxygen, and, accordingly, fossil content. Most nonmineralized metazoan fossils occur where favorable preservational environments are closely interbedded with other types of beds.

"couplets" ranging from 1 to 12 mm in thickness, with no apparent size or compositional grading; and 4, uninterrupted vertical persistence for tens of meters of section, indicating sustained low-energy deposition below the influence of storm waves. The "couplets" of the Wheeler Formation are interpreted as the distal expression of gravity-dominated depositional events spilling off of the adjacent ramp—however, they also may contain a hemipelagic component. Some evidence for bottom-flowing currents is present, including transported (see below) and current aligned fossils (Rees, 1986), and rare tool marks.

The availability or lack of dissolved oxygen in bottom waters during deposition is a critical issue. In order to assess paleo-redox conditions, an ichnological model was applied (Savrda and Bottjer, 1986), which correlates increasing depth and extent of bioturbation to increasing availability of dissolved oxygen of bottom waters. In modern environments, anoxic conditions are characterized by a complete absence of bioturbation (ichnofabric index (i.i.)1), whereas well-oxygenated environments are characterized by well-developed ichnofabrics (i.i.4-5), and destruction of most

primary sedimentary structures (Savrda et al. 1984). Extrapolating ichnological models to Cambrian sediments requires caution, because the infaunal habitat was incompletely developed at this time (Droser and Bottjer, 1988). Thus, this model was used as a relative tool, to compare oxygen levels among beds within the Wheeler Formation. This model was applied on a bed-to-bed basis in order to develop relative oxygen curves at a millimeter scale for each of the continuously sampled intervals. The Wheeler Formation is inferred to have had a complex redox history during deposition, characterized largely by oxygen-deficient bottom water conditions that, at times, were sufficient to permit benthic colonization by epifaunal and infaunal organisms. Many sampled intervals show sustained bottom water anoxia, whereas others show dynamic shifts from inferred anoxic to dysoxic conditions at a centimeter to decimeter scale (Figure 1).

## PALEOECOLOGY

In the >3000 individual beds analyzed, Burgess Shale-type preservation occurs exclusively in the absence of bioturbation (i.i.1). Thus, it is inferred that in the Wheeler

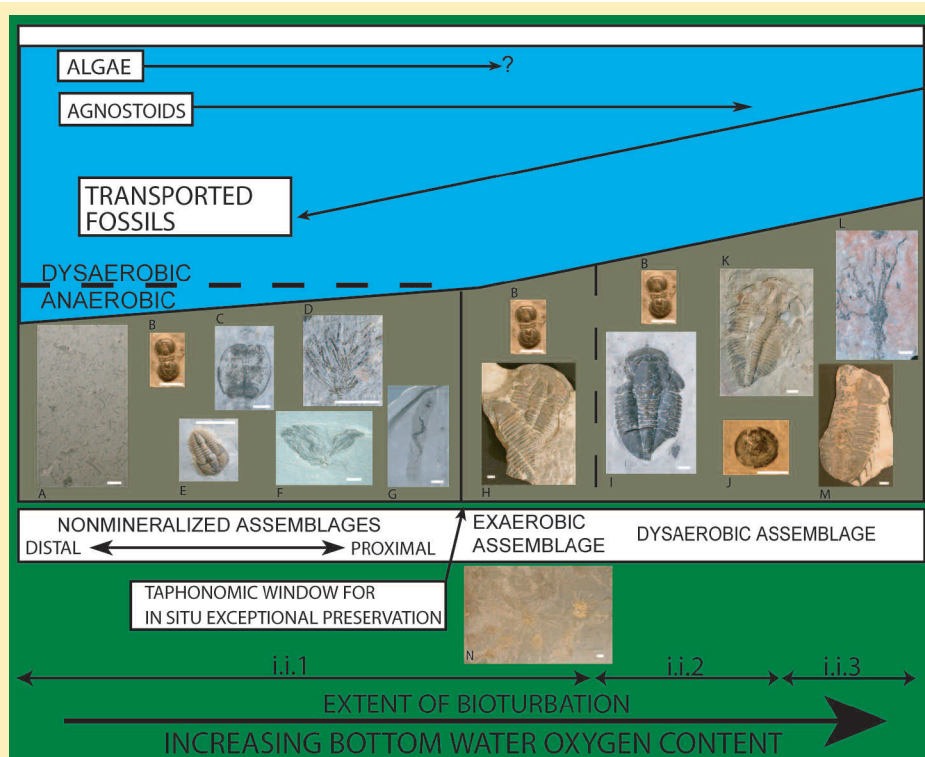


Figure 2. Paleoeological reconstruction of the Wheeler Formation showing bottom water oxygen control over the distributions of fossils found in the basinal mudrock facies. Distal nonmineralized assemblages are characterized by A, bedding planes covered in algae (fragmentary or small), some belonging to the genera *Marpolia* and *Morania*. B. *Peronopsis*, and other agnostoid trilobites occur in all assemblages, indicative of a pelagic mode of life, unrelated to benthic conditions. Proximal nonmineralized assemblages are characterized by larger and more complete fossils: C. Articulated carapace of a phyllocarid arthropod. D. *Yuknessia simplex*, a nonmineralized alga. E. *Brachyaspidium microps*, a pelagic trilobite. F. *Marpolia spissa*, a nonmineralized alga. G. Undetermined metazoan showing gut tract. Exaerobic assemblages contain *Elrathia kingii* (H), in addition to occasional pelagic fossils. Dysaerobic assemblages contain a more diverse skeletonized fauna, including: I. *Asaphiscus wheeleri*. J. *Acrothele*?, K. *Alokistocare*. L. *Gogia spiralis* (eocrinoid). M. *Olenoides*. Rarely, nonmineralized preservation occurs in situ when sharp shifts in bottom water oxygen content occur: N. Association of *Choa*. All scale bars are 5 mm.

Formation, this style of preservation occurs only under anoxic bottom waters, uninhabitable by benthic metazoans. Whereas this finding offers little hope for the possibility of resolving distinct ecological assemblages within the nonmineralized faunas, microstratigraphic patterns provide some insight. Nonmineralized fossils occur along a gradient ranging from abundant fragmented and diminutive forms to larger and more complete forms, which occur in lower densities. Microstratigraphic proximity of any given horizon bearing nonmineralized preservation to bioturbated (oxic) horizons is a reliable indicator of what type of nonmineralized assemblages will be present. Intervals representing accumulation under sustained bottom water anoxia contain nonmineralized preservation of small and/or disarticulated forms, dominated by algae with rare metazoans, in each individual bed, often through hundreds of sequential beds (Figure 1A). Intervals bearing nonmineralized preservation that are interbedded closely (<10 cm) with bioturbated

horizons reflect oscillating bottom water oxygen content, and contain larger and more complete nonmineralized fossils, including a significant proportion of metazoans (Figure 1B). Thus, the observed gradient in size and articulation of nonmineralized fossils is inferred to be related to distance of transport. Intervals characterized by sustained anoxia represent accumulation sites distal to the anoxic-oxic boundary, and thus, to habitable benthic environments from which the nonmineralized fossils were sourced. Intervals occurring in close microstratigraphic proximity to habitable benthic environments are inferred to represent accumulation sites proximal to oxic benthic environments, and thus contain larger and more complete forms (see Figure 2). This proximal-distal gradient in Burgess Shale-type preservation ranges from distal environments to the edge of oxic benthic environments, where, most rarely, in situ preservation of nonmineralized forms does occur, when abrupt shifts to bottom water anoxia coincide with burial of benthic forms.

Such occurrences provide the best hope of understanding elements of the Burgess Shale biota in an ecological context, and may be sought for further study by targeting such environments for search.

Although BST deposits are best known for the nonmineralized fossils they preserve, most also contain diverse faunas of skeletonized forms. In the Wheeler Formation, skeletonized faunas are dominated by trilobites, and also include acrotretid brachiopods and echinoderms. The best-known fossil from the Wheeler Formation is the trilobite *Elrathia kingii*, which is found in collections around the world. Despite a narrow geographic range, *E. kingii* is sufficiently abundant to be distributed commercially because it occurs in dense associations of up to 500 complete individuals per m<sup>2</sup>, and it is typically coated with cone-in-cone calcite on the ventral side, allowing easy extraction from the rock. Microstratigraphic analyses revealed that *E. kingii* occurs in monospecific associations, although *E. kingii* commonly occurs in hand samples with other faunas that occur on other bedding planes (Gaines and Droser, 2003). Microstratigraphic data also reveal that most (93.6%) *E. kingii* occurrences are in unbioturbated beds that are in close vertical proximity (mm-cm) to beds bearing nonmineralized preservation, and also closely adjoin beds that contain weak to moderate levels of bioturbation. Because it occurs prominently at the transitions from beds deposited under anoxic conditions to those deposited under oxic conditions, it is inferred that *E. kingii* occupied a niche habitat at the edge of oxygenated bottom waters, below the oxygen levels required to support an infauna (Gaines and Droser, 2003). This manner of occurrence is consistent with an “exaerobic zone” lifestyle (Savrda and Bottjer, 1987), indicating that *E. kingii* may have used sulfur bacteria as a primary food source. Chemoautotrophic sulfur bacteria occur in abundance at this boundary today, where free sulfides in anoxic bottom waters mix with minimally oxygenated bottom waters (Figure 3). The ready availability of sulfur bacteria as a food source provides the most plausible explanation for adaptation to a marginal, oxygen-stressed habitat. Sulfur bacteria have been proposed as a primary food source for other trilobites (Fortey, 2000), and the morphology of *E. kingii* is consistent with these interpretations, as *E. kingii* possesses a number of attributes considered advantageous for life in oxygen-depleted environments. This finding indicates that non-phototrophic-based ecosystems were in place early in the history of animal life. *E. kingii* also serves as an excellent pale-

environmental indicator in the Wheeler Formation, marking the transition between oxic and anoxic benthic conditions, otherwise irresolvable in the field. The possibility that the exaerobic niche may have been occupied in other Cambrian environments holds great paleoecological significance.

Both nonmineralized fossil assemblages and *E. kingii* associations are characteristic of specific, yet different, bottom water oxygen conditions, and both occur in unbioturbated (i.i.1) beds. A third assemblage type, microstratigraphically distinct from horizons bearing nonmineralized preservation as well as from those bearing *E. kingii*, is characterized by the presence of weak to moderate levels of bioturbation (i.i. 2-3), interpreted to signify dysoxic conditions (Figure 2). This assemblage is dominated by large (>3 cm) trilobites, most prominently *Asaphiscus wheeleri*, and also includes acrotretid brachiopods and the eocrinoid *Gogia*. Orientation and evidence from molt assemblages indicates that these faunas occur in situ, however in lower densities than either the *E. kingii* or nonmineralized fossil associations. Further bed-to-bed-scale work holds the promise of resolving discrete paleoecological associations within this assemblage. A significant fauna of pelagic trilobites is also found in the Wheeler Formation, including a diverse assemblage of agnostoids (Robison, 1964). The diminutive non-agnostoid trilobites *Jenkinsonia varga* and *Brachyaspidion microps* are also interpreted as pelagic on the basis of biofacies-crossing distributions and their common presence in beds representing deposition under uninhabitable (anoxic) benthic conditions.

We infer that benthic redox conditions acted as a first-order control over fossil content in the Wheeler Formation, regulating the primary distributions of organisms as well as their preservation (Figure 2). Importantly, while all three types of assemblages (nonmineralized, *E. kingii*, dysaerobic) may occur within a single, narrow microstratigraphic interval (millimeters-centimeters) at the scale of a hand-sample, they represent discrete associations that occurred under demonstrably different benthic conditions.

## PRESERVATION

Specific mechanisms of nonmineralized fossil preservation are a subject of some debate. Whereas mineral-replacement of some non-biomineralized tissues occurs in some deposits (e.g., Emu Bay Shale of Australia; Briggs and Nedin, 1997; and Chengjiang deposit of China; Zhu et al., 2005), the most common type of preservation of nonmineralized tissues

in BST deposits may be “Burgess Shale-type preservation” (Butterfield, 1995, 2003) of fossils as two-dimensional carbon films, although associated mineral films also may be present (Orr et al., 1998). Curiously, this type of preservation is insignificant as a means of preserving benthic faunas after the middle Cambrian. While some types of mineral replacement of non-biomineralized tissues have been explained using actualistic models (e.g., Briggs and Kear, 1994), the causes of “Burgess Shale-type” preservation have typically been addressed using theoretical models.

Butterfield (1995) proposed that highly reactive clay minerals may have been commonplace on continental margins during some intervals of time and facilitated Burgess Shale-type preservation through adsorption of decay-inducing enzymes. This hypothesis was not supported by a metamorphic study of the Burgess Shale (Powell, 2003), which concluded that the original mineralogic composition of that unit was not unusual, and did not include any highly-reactive mineral species. Petrovich (2001) suggested that, under suboxic conditions, iron ions (abundant in clay-rich marine sediments) are strongly adsorbed onto chitin and other organic biopolymers, and may have prevented decay of these select tissues by coating them and thereby physically blocking the enzymatic action of microbial decomposers. However, this model predicts that such preservation should be common in clay-rich, oxygen-deficient strata throughout the Phanerozoic. Both models, which invoke molecular-scale chemical interactions, do not provide comprehensive explanations of this phenomenon, and are problematic for the reasons described above.

Data obtained through intensive study of the Wheeler Formation were also applied towards the development of a new hypothesis for

Burgess Shale-type preservation (Gaines et al., 2005). This model unites micron-scale diagenetic processes involved in preservation with primary physical features of the depositional environment, allowing predictions to be readily applied to testing in other deposits. Burgess Shale-type preservation in the Wheeler Formation uniformly occurs in exclusively fine-grained sediments, lacking silt, fecal pellets, skeletal microfossils, and coarser particles. The close proximity of the depositional environment to a carbonate platform resulted in mixed carbonate-clay sediments, and facilitated ubiquitous early diagenetic carbonate cements characteristic of Wheeler mudrocks (Gaines et al., 2005). These cements occur as micron-sized pore filling cements and cone-in-cone cements around pre-existing carbonates, including trilobite carapaces or micritic horizons. Isotopic ( $\delta^{13}\text{C}$ ) and petrographic evidence indicates that cements were emplaced early in the diagenetic history and were derived from a detrital carbonate precursor (Gaines et al., 2005). This model proposes that preservation of nonmineralized tissues in the Wheeler Formation resulted from a combination of influences that reduced permeability and thus lowered oxidant flux, which in turn may have acted to restrict microbial decomposition of some nonmineralized tissues. The absence of coarse grains (>50  $\mu\text{m}$ ) and skeletonized microfossils provided very low original porosity. Near-bottom anoxia prevented sediment irrigation by restriction of bioturbation. Reducing conditions near the sediment-water interface also may have acted to deflocculate aggregations of clay minerals, resulting in low permeability face-to-face contacts (Moon and Hurst, 1984). Abundant early diagenetic pore-occluding carbonate cements are suggested to have contributed significantly to occlusion of remaining porosity, halting oxidant flux into

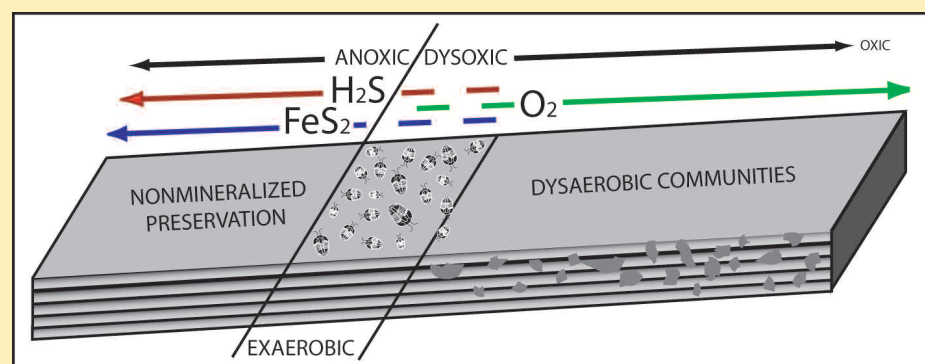


Figure 3. A. Schematic diagram illustrating the “exaerobic” concept of Savrda and Bottjer (1987). Movement of the anaerobic/dysaerobic boundary across the seafloor over time result in close interleaving of exaerobic beds with beds accumulated under anaerobic conditions, as well as under more oxic conditions, as shown in B, a 10-cm microstratigraphic log. (Triangles=cone-in-cone calcite; arrows=nonmineralized preservation; blue ovals = *E. kingii* nodules; “Squiggles”=burrows).

the sediments, restricting microbial decomposition and facilitating carbonaceous preservation of macrofossils. Fe-organic interactions (Petrovich, 2001) or clay-organic interactions (Butterfield, 1995) may have also operated at molecular scale within the Wheeler sediments and thereby provided a favorable early burial environment at the micron scale and above.

## TOWARDS A GLOBAL PICTURE: REMAINING CHALLENGES

In the Wheeler Formation, several regional and global factors were important in promoting the conditions described above, and thus, these factors may be relevant to the global distribution of Burgess Shale-type deposits. First, the depositional environment occurred offshore of a broad (~300 km) carbonate platform, which sequestered coarse siliciclastics inboard, and resulted in exclusively fine-grained, mixed carbonate-siliciclastic sediments with low original porosities and the potential for early carbonate cementation. Relatively high sea levels and broad passive margins of the middle Cambrian (Brasier and Lindsay, 2001) were clearly an important factor, resulting in the migration of this distal depositional environment onto continental crust, where sediments have long-term preservation potential. Secondly, oxygen-limited bottom waters that lay just outboard of the platform margin were important in providing a close juxtaposition of anoxic and oxic benthic environments. The location of this boundary on the slope is also important as it promotes downslope transportation of organisms from the living environment to the (uninhabitable) preservational environment, and, in this case, it places the boundary over sediments favorable to preservation, described above. The incursion of oxygen-deficient water masses onto the slope at this time has been linked to restricted seaways, tropical conditions, and transgressive episodes (Landing, 2001). A third important aspect is the absence of skeletal microfossils from the locus of deposition. In the Holocene, skeletal microorganisms are particularly abundant in shelf edge settings, and their abundance is positively correlated with both porosity and permeability of sediments (Kraemer et al., 2000), however, the oldest microfossil oozes do not occur until the late Cambrian (Tolmacheva et al., 2001), indicating a rise in abundance only at this time. While these conclusions are drawn from a single deposit, these aspects of the Wheeler Formation's primary depositional environment are the result of regional and global phenom-

na, and may be common to the Burgess Shale, as well as to other BST deposits.

Field-based and lab-intensive investigations of other BST deposits, conducted at an appropriate scale, may provide insight not available from studies of individual taxa alone. Further studies at this scale are needed. Additionally, the root causes of widespread oxygen deficiency in early and middle Cambrian slope environments warrant further investigation. Did these conditions result from periodically enhanced flux of organic matter to the seafloor, restricted circulation under climatic optima (Landing, 2001), low-lying continents at tropical latitudes, or some combination of these and other factors? Finally, the paleoecology of these most diverse Cambrian faunas deserves further study. These results suggest that discrete associations of fossils within apparently homogenous, fine-grained deposits may be resolved at a fine scale and linked to specific paleoenvironmental conditions. While results from the Wheeler Formation indicate that most nonmineralized faunas are transported assemblages of limited ecologic utility, these results provide framework criteria for their evaluation and suggest that associated assemblages of skeletonized fossils may provide significant opportunity for in situ paleoecologic study. As Burgess Shale-type deposits should be characterized by occurrence at or near the benthic redox (anoxic-dysoxic) boundary, they also present an environmental window in which to evaluate the possibility that the non-phototrophic, exaerobic lifestyle may have been widespread during the "Cambrian explosion."

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## REFERENCES:

Allison, P.A., and Briggs, D.E.G., 1993, Exceptional fossil record: Distribution of soft-tissue preservation through the Phanerozoic: *Geology*, v. 21, p. 527-530.  
 Babcock, L.E., 2003, Trilobites in Paleozoic predator-prey systems, and their role in reorganization of early Paleozoic ecosystems, in Kelley, P.H., Kowalewski, M., and Hansen, T.A., eds., *Predator-Prey Interactions in the Fossil Record*, Kluwer Academic/Plenum Publishers, New York, p. 55-92.  
 Babcock, L.E., Zhang, W., and Leslie, S.A., 2001, The Chengjiang Biota:

Record of the Early Cambrian diversification of life and clues to exceptional preservation of fossils: *GSA Today*, v. 11, p. 4-9.  
 Brasier, M.D., and Lindsay, J.F., 2001, Did supercontinental amalgamation trigger the "Cambrian Explosion"? in Zhuravlev, A.Y., and Riding, R., eds., *The Ecology of the Cambrian Radiation*, Columbia University Press, New York, p. 69-89.  
 Briggs, D.E.G., and Kear, A. J., 1994, Decay and mineralization of shrimps: *Palaios*, v. 9, p. 431-456.  
 Briggs, D.E.G., and Nedin, C., 1997, The taphonomy and affinities of the problematic fossil *Myoscolex* from the Lower Cambrian Emu Bay Shale of South Australia: *Journal of Paleontology*, v. 71, p. 22-32.  
 Butterfield, N.J., 1995, Secular distribution of Burgess Shale-type preservation: *Lethaia*, v. 28, p. 1-13.  
 Butterfield, N.J., 2003, Exceptional fossil preservation and the Cambrian explosion: *Integrative & Comparative Biology*, v. 43, 166-177.  
 Conway Morris, S., 1986, The community structure of the Middle Cambrian phyllopod bed (Burgess Shale): *Palaentology*, v. 29, p. 423-467.  
 Conway Morris, S., 1989, The persistence of Burgess Shale-type faunas: implications for the evolution of deeper-water faunas: *Transactions of the Royal Society of Edinburgh: Earth Sciences*, v. 80, p. 271-283.  
 Conway Morris, S., 1998, *The Crucible of Creation*: Oxford University Press, Oxford, 242 p.  
 Droser, M.L., and Bottjer, D.J., 1988, Trends in depth and extent of bioturbation in Cambrian carbonate marine environments, western United States: *Geology*, v. 16, p. 233-236.  
 Elrick, M., and Hinnov, L.A., 1996, Millennial-scale climate origins for stratification in Cambrian and Devonian deep-water rhythmites, western USA: *Palaogeography, Palaeoclimatology, Palaeoecology*, v. 123, p. 353-372.  
 Fortey, R., 2000, Oldest trilobites: The oldest known chemoautotrophic symbionts: *Proceedings of the National Academy of Science*, v. 97, p. 6574-6578.  
 Gaines, R.R., and Droser, M.L., 2003, Paleoecology of the familiar trilobite *Elnathia kingii*: an early exaerobic zone inhabitant: *Geology*, v. 31, p. 941-944.  
 Gaines, R.R., Kennedy, M.J., and Droser, M.L., 2005, A new hypothesis for organic preservation of Burgess Shale taxa in the middle Cambrian Wheeler Formation, House Range, Utah: *Palaoclimatology, Palaogeography, Palaeoecology*, v. 218.  
 Hagadorn, J.W., 2002, Burgess Shale-type localities: The global picture, in Bottjer, D.J., Etter, W., Hagadorn, J.W., and Tang, C.M., eds., *Exceptional Fossil Preservation*, Columbia University Press, New York, p. 91-116.  
 Kraemer, L.M., Owen, R.M., and Dickens, G.R., 2000, Lithology of the upper gas hydrate zone, Blake Outer Ridge: a link between diatoms, porosity, and gas hydrate: *Proceedings of the Ocean Drilling Program, Scientific Results*, v. 164, p. 229-236.  
 Landing, E., 2001, "Burgess Biotas" and episodic slope and epic seafloor dysaerobia in the Late Precambrian-Paleozoic: *Geological Society of America Abstracts with Programs*, v. 33, p. 38.  
 Moon, C.F., and Hurst, C.W., 1984, Fabric of mud and shales: an overview, in Stow, D.A.V., and Piper, D.J.W. (Eds.), *Fine-grained Sediments*, Geological Society Special Publication v. 15, p. 579-593.  
 Orr, P.J., Briggs, D.E.G., and Kearns, S.L., 1998, Cambrian Burgess Shale animals replicated in clay minerals: *Science*, v. 281, p. 1173-1175.  
 Petrovich, R., 2001, Mechanisms of fossilization of the soft-bodied and lightly armored faunas of the Burgess Shale and of some other classical localities: *American Journal of Science*, v. 3001, p. 683-726.  
 Potter, P.E., Maynard, J.B., and Pryor, W.A., 1980, *Sedimentology of Shale*, Springer-Verlag, New York, 306 p.  
 Powell, W., 2003, Greenschist-facies metamorphism of the Burgess Shale and its implications for models of fossil formation and preservation: *Canadian Journal of Earth Sciences*, v. 40, p. 13-25.  
 Rees, M.N., 1986, A fault-controlled trough through a carbonate platform: the middle Cambrian House Range embayment: *GSA Bulletin*, v. 97, p. 1054-1069.  
 Robison, R.A., 1964, Late Middle Cambrian faunas from western Utah: *Journal of Paleontology*, v. 38, p. 510-566.  
 Robison, R.A., 1991, Middle Cambrian biotic diversity: examples from four Utah Lagerstätten: in Simonetta, A.M., and Conway Morris, S., eds., *The Early Evolution of the Metazoa and the Significance of Problematic Taxa*, Cambridge University Press, Cambridge, p. 77-98.  
 Svrda, C.E., and Bottjer, D.J., 1986, Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters: *Geology*, v. 14, p. 306-309.  
 Svrda, C.E., and Bottjer, D.J., 1987, The exaerobic zone, a new oxygen-deficient marine biofacies: *Nature*, v. 327, p. 54-56.  
 Svrda, C.E., Bottjer, D.J., and 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: *American Association of Petroleum Geologists Bulletin*, v. 68, p. 1179-1192.  
 Schieber, J., 2003, Simple gifts and buried treasures- Implications of finding bioturbation and erosion surfaces in black shales: *The Sedimentary Record*, v. 1, p. 4-8.  
 Seilacher, A., 1997, The meaning of the Cambrian explosion: *Bulletin of the National Museum of Natural Science, Taiwan*, v. 10, p. 1-10.  
 Tolmacheva, T.J., Danelian, T., and Popov, L.E., 2001, Evidence for 15 m.y. of continuous deep-sea biogenic siliceous sedimentation in early Paleozoic oceans: *Geology*, v. 29, p. 755-758.  
 Zhu, M.Y., Babcock, L.E., and Steiner, M., 2005, Fossilization modes in the Chengjiang Lagerstätte (Cambrian of China): testing the roles of organic preservation and diagenetic alteration in exceptional preservation: *Palaogeography, Palaeoclimatology, Palaeoecology*, 218.  
 Zhuravlev, A.Y., and Riding, R., eds., 2001, *The Ecology of the Cambrian Radiation*: Columbia University Press, New York, 525 p.