

INTERPRETING THE PALEOENVIRONMENTAL CONTEXT OF MARINE SHALES DEPOSITED
DURING THE CAMBRIAN RADIATION: GLOBAL INSIGHTS FROM SEDIMENTOLOGY,
PALEOECOLOGY, AND GEOCHEMISTRY

by

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A Dissertation Submitted in

Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

in Geosciences

at

The University of Wisconsin-Milwaukee

December 2012

ABSTRACT

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The University of Wisconsin-Milwaukee, 2012
Under the Supervision of Professor Stephen Q. Dornbos

Many Cambrian marine shales are traditionally thought to have been deposited under dysoxic or anoxic conditions based upon interpretations of sedimentological and ichnological fabrics. Recently a number of geochemical studies have suggested the opposite, that some Cambrian marine shales were deposited under slightly oxic to well-oxygenated conditions. Despite the significant implications redox conditions have for the paleoenvironment, paleoecology, and taphonomy of Cambrian shales, rarely are these disparate sedimentological and geochemical approaches combined for direct comparisons in a singular study of Cambrian shales. A multidisciplinary approach is used here, combining sedimentological, paleoecological, and geochemical approaches, for re-interpreting the paleoenvironmental conditions of numerous Cambrian marine shales associated with exceptional fossil preservation. Sedimentological analyses indicate that most shales generally lack bioturbation (average ichnofabric index ~ 1), with some evidence for the presence of microbial mats, suggesting that depositional environments were dominated by Proterozoic-style substrates. An analysis of the morphological adaptations of marine benthic communities preserved in Cambrian shales demonstrates that most faunas exhibit a mixture of Proterozoic- and Phanerozoic-style adaptive strategies, which is consistent with expectations from the Cambrian substrate revolution. Geochemical analysis indicates that Cambrian shales were deposited under

generally oxic conditions and not under anoxic conditions as traditionally thought. This result supports the sedimentological and paleoecological interpretations for the presence of Proterozoic-style substrates in these paleoenvironments. Oxic depositional conditions pose difficulties for taphonomic models where anoxia is a prerequisite for BST preservation. As these geochemical results are consistent with similar geochemical studies of the Burgess, Kinzers, and Emu Bay Shales, serious consideration must be made as to the validity of anoxia-based taphonomic models and oxic-based taphonomic models should be considered. The unique geochemical conditions found within microbially mediated substrates may offer a viable pathway for BST preservation under oxic conditions, as microbial mats were likely associated with Proterozoic-style substrates in Cambrian shales.

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CHAPTER 1: INTRODUCTION

Early-to-middle Cambrian marine shales are significant for two reasons: 1) they were deposited during the Cambrian Radiation, a period of major ecological and environmental upheaval in marine settings; and 2) many are associated with soft-bodied preservation of early metazoans, most notably Burgess-Shale-type (BST) faunas, that provide us with high fidelity paleoecological information for animals living during the Cambrian Radiation. This dissertation investigates the paleoenvironments of Cambrian marine shales in an attempt to understand how the physical nature of marine substrates may have influenced the development of benthic faunas and BST preservation during this time. Relative intensities of bioturbation are measured via ichnofabric analysis to estimate the extent of infaunal colonization within the Cambrian substrate and directly compared to estimates of redox conditions in the bottom water via geochemical analysis to determine the dominant substrate conditions at the time of deposition. A paleoecological analysis was also conducted using literature review of the benthic genera preserved in sixteen Cambrian and Ordovician exceptionally preserved fossil assemblages to assess how substrate conditions controlled morphological development of benthic metazoans through the Cambrian. This multidisciplinary approach demonstrates that apparent discrepancies between these techniques reported in literature can be explained as a result of the unique environmental conditions associated with the Cambrian Radiation.

1.1 The earliest fossil record and the Cambrian Radiation

An examination of the geologic record finds that the Cambrian Radiation marks the most commonly accepted first appearance of modern metazoan body fossils in the geologic record. The record of life on Earth extends back much further. Stromatolites, laminated carbonate structures often identified as having been formed through an accretionary process controlled by the presence of microbes, first appear ~3500Ma during the Archean (Walter 1983). Many of these very early stromatolites lack associated microfossils, and thus their origins are controversial; however, later stromatolite forms exhibit organic structures that suggest multispecific communities of single-celled organisms were forming laminated stromatolites by at least 2724Ma before present (Lepot et al. 2008). Similar microbial communities, constructing thick “mats” of laminated cohesive material through a process of binding-and-trapping sediment, were ubiquitous in shallow marine environments at around the same time (Horodyski 1993; Fedonkin et al. 1994; Xiaoying et al. 2008). These stromatolites and microbial mats were the dominant preserved biological presence on Earth until the appearance of complex multicellular life forms during the later Neoproterozoic, and would still retain relative dominance in the epifaunal realm until the Neoproterozoic-Cambrian transition (Bland 1984; Runnegar and Fedonkin 1992; Hagadorn and Bottjer 1987; Gehling 1999).

The late Neoproterozoic Ediacaran Period saw the appearance of the Ediacaran fauna beginning at ~575Ma, named for the Ediacara Hills of southwest Australia where the

taxa were first described. The fauna includes a bewildering menagerie of evolutionary design, many of which still confound paleontologists: the flat, quilted body of *Dickinsonia* (Fig. 1.1a), the repetitive, tessellating morphology of the rangeomorphs (Fig. 1.1b, d), the tri-lobed symmetry exhibited by *Trichoniscus* (Fig. 1.1c), and taxa best known by the descriptions “Triangle” and “Christmas Tree” (Narbonne 1998; Clapham and Narbonne 2003; Bamforth et al. 2008; Braiser 2008; Narbonne et al. 2009).

Associated with the Ediacaran fauna are simple locomotion trace fossils and resting traces that likely represent early bilaterians (Fig. 1.1e,f) (Narbonne 1998). Ediacarans are generally accepted as complex multicellular organisms, but their relationship with modern animals is unclear, and members of the biota have been variously interpreted over the years as cnidarians (Sprigg 1947; Droser and Gehling 2008), algae (Bergstrom 1991), protists (Zhuravlev 1993; Duval and Margulis 1995), (possibly distant) relatives to modern animals (Buss and Seilacher 1994; Waggoner 1998), a unique form of “metacellular” multicellular critter (McMenamin 1986), and—possibly most famously—as a class of organisms, the Vendobionta, that are completely unrelated to any other living metazoan (Seilacher 1992). Ediacaran morphologies are difficult to shoehorn into any extant phyla, and some—like the rangeomorphs—defy comparison to modern metazoans.

Ediacaran community ecology also appears to be in stark contrast to later metazoan communities that emerged from the Cambrian Explosion. While some

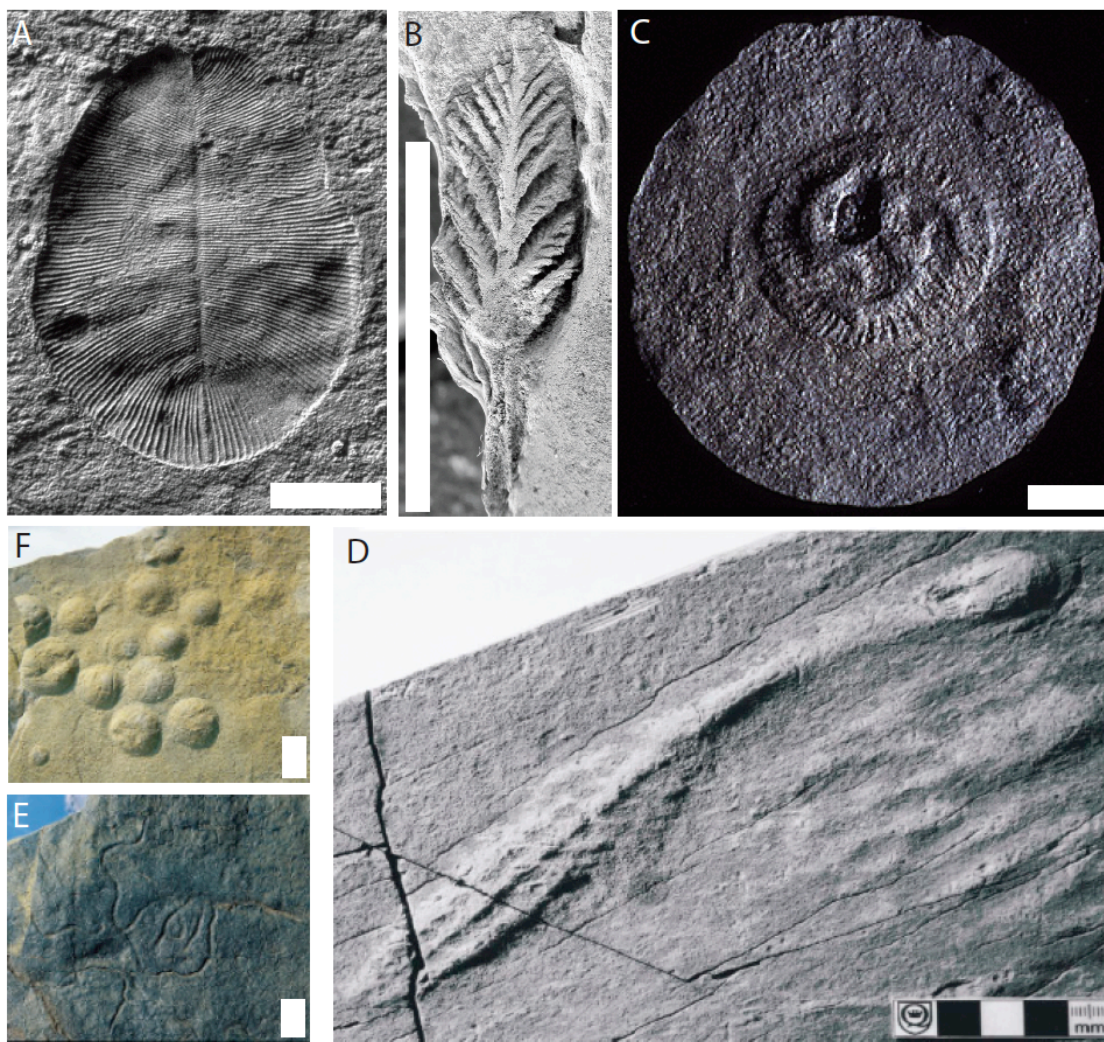


Figure 1.1. Members of the Ediacaran fauna. A: *Dickinsonia* (modified from Grazhdankin 2004); B: *Avalofractus abaculus* (modified from Narbonne et al. 2009); C: *Tribrachidium* (modified from Peabody Museum of Natural History); D: *Charniodiscus spinosus* (modified from LaFlamme et al. 2004); E: simple meandering trace fossil (modified from Narbonne 1998); F: cnidarian resting traces (modified from Narbonne 1998). All scale bars except in D = 1cm. Scale bar in D = 5cm.

difficult to shoehorn into any extant phyla, and some—like the rangeomorphs—defy comparison to modern metazoans.

Ediacaran community ecology also appears to be in stark contrast to later metazoan communities that emerged from the Cambrian Explosion. While some characteristics of Ediacaran Biota community ecology appear surprisingly complex, such as the presence of epifaunal tiering (Narbonne 1998; Clapham and Narbonne 2003), Ediacaran communities exhibit a number of features that are uncharacteristic of later animal communities: 1) many Ediacarans exhibit unusual body plans that are difficult to resolve within modern phyla (LaFlamme et al. 2004, but see above); 2) Ediacarans were generally soft-bodied and lacking hard parts (Seilacher 1992; Narbonne 1998; Waggoner 1998); 3) Ediacaran communities present rare evidence for predation and predator-prey relationships (Stanley 1973; McMenamin 1986), with one notable exception being the presence of suspected bore holes in specimens of *Cloudina* (Bengtson and Zhao 1992); 4) Most Ediacarans appear to have been immobile, or only facultatively mobile, although simple meandering traces and feeding scratch marks do occur (Narbonne 1998); 5) Ediacaran substrates were extensively colonized by microbial mat communities (Narbonne 1998; Bottjer et al. 2000; Dornbos et al. 2005); 6) Bioturbation levels were very low (Narbonne 1998; Dornbos et al. 2005; although see Rogov et al. 2012 for dissenting discussion) and burrowing organisms much less effective at modifying their environment than their modern counterparts, burrowing at or very near the sediment surface (Droser et al. 1999, 2002; Jensen 2003; Gingras et al. 2011). It

seems clear that, whatever forms of life Ediacarans represent, their ecology is not analogous to modern animal communities.

The Cambrian Radiation produced marine communities that, for the first time in the geologic record, appear familiar to the modern ecologist. Predation is widespread, establishing predator-prey relationships and early trophic food webs (Nedin 1999; Vannier and Chen 2002; Vannier and Chen 2005; Chen et al. 2007). Biomineralization is extensive and common across nearly all phyla (Matthews and Missarzhevsky 1975; Bengtson 1994). Bioturbation is widespread, leading to significant changes in substrate conditions (Bottjer et al. 2000) and the increasing complexity of trace fossil forms indicates that mobile behaviors were already well established (Jensen 2003). The community itself was now mainly composed of recognizable representatives of modern extant phyla, and Ediacarans had disappeared. By the end of the Cambrian many ecologic innovations that are hallmarks of modern metazoan communities were in place.

The cooperative rise of four ecologic innovations—predation, biomineralization, mobility/burrowing, and the evolution of macroscopic sensory organs (e.g., eyes)—was no accident, but certainly the expression of the early biological arms race between predator and prey and between trophic competitors within the same marine communities. Escalating competition for trophic resources is already apparent by the Ediacaran, as tiering structures were fairly well developed (Clapham and Narbonne 2003). The added energy expenditures required to elevate feeding structures to new

tiering levels suggests that Ediacarans were exploring the means to exploit untapped or underutilized trophic resources. Animal communities expanded this tiering concept by exploring the infaunal realm for buried organic sources (via bioturbation); and went beyond the two-dimensional concept of tiering by also exploiting other animals as a food source (predation). Once established, these ecological innovations had a reciprocal effect on each other: predation escalated the defensive measures of prey species, leading to increased adaptation of biomineralization and hard skeletons, which in turn drove the evolution of new predatory behaviors; burrowing behavior would be adapted as an advantage to avoiding predators, and predators no doubt learned burrowing strategies to exhume prey, and bioturbation intensity increased as tiering structures became more complex as animals continually searched for new trophic levels to obtain food. Once established, these ecological interactions help to construct Phanerozoic community ecologies within a geologically short period of time.

As burrowers and bioturbation played a critical role in the development of modern marine ecosystems, they also played a significant role in the evolution of the marine benthos. Increasing bioturbation would inflict major changes in the physical nature of marine substrates, triggering two of the most ecological-and-evolutionary influential events of the Cambrian Radiation: the agronomic and Cambrian substrate revolutions (Seilacher and Pflüger 1994; Bottjer et al. 2000).

1.2 The Agronomic Revolution

Single-celled organisms were the dominant life form for most of Earth's history, and microbial communities were significant agents in the development of substrates in shallow marine environments. The construction of mm-thick, cohesive, sticky, layered mat structures by these microbial communities mitigated substrate deposition and in part controlled the geochemical processes occurring within the infaunal realm (Fig. 1.2). Without competition from other organisms, these microbial mats proliferated during the Proterozoic and the sedimentary structures of Proterozoic units reflect this: "elephant skin", wrinkle structures, and wavy-crinkly laminae are interpreted as organosedimentary structures influenced by microbial activity (Knoll 1985; Runnegar and Fedonkin 1992; Hagadorn and Bottjer 1997; Gehling 1999; Schieber 1999; Schieber 2007). The presence of microbial mats is associated with a distinct character of "Proterozoic-style" substrate: substrates were firm but unlithified, with a distinct water-sedimentary boundary, low water and oxygen content in sediments, and elevated levels of hydrogen sulfide resulting from the activities of sulfide-reducing bacteria (van Gemerden 1993; Seilacher and Pflüger 1994;; Bailey et al. 2006).

Microbially mediated substrates were also lacking in bioturbation, a key component of modern marine substrates. Prior to the Cambrian and during much of the Proterozoic burrowing and bioturbated sediments (and the organisms associated with this behavior) were absent from normal shallow shelf marine settings (Seilacher and Pflüger 1994; Hagadorn and Bottjer 1997; Narbonne 1998; McIlroy and Logan 1999;

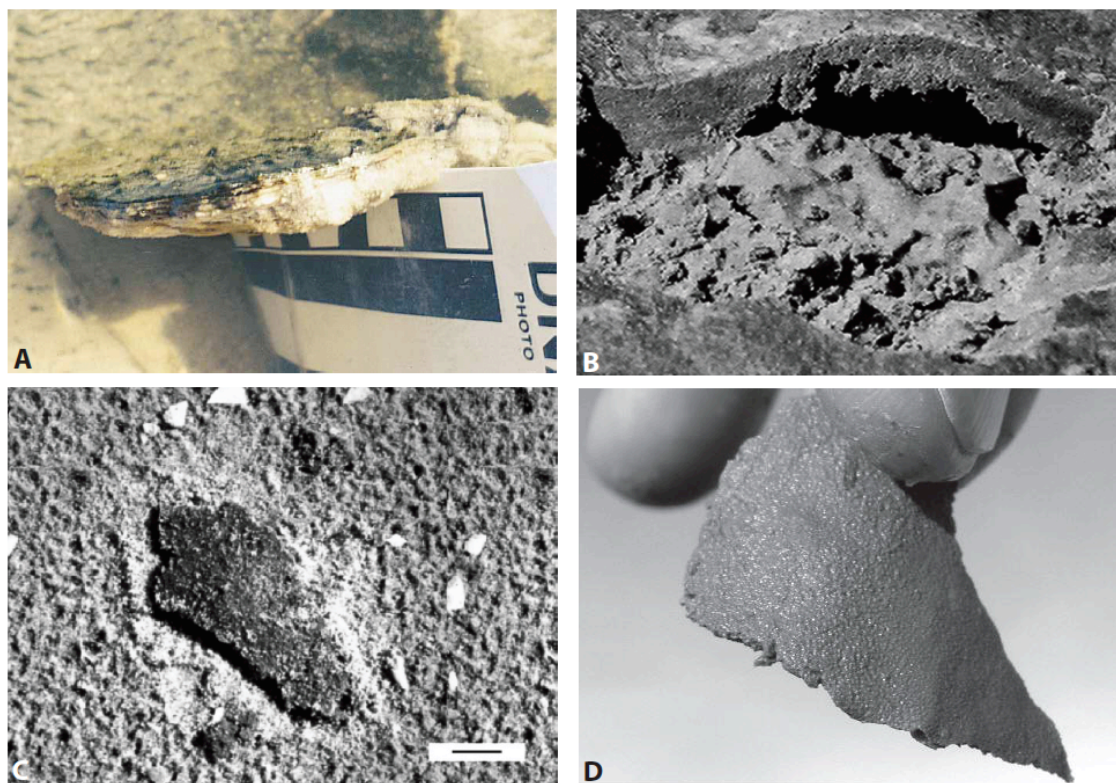


Figure 1.2. Modern microbial mats. A: Microbial mat in profile. Note wrinkled surface and cohesiveness of disturbed section of mat (modified from Hagadorn and Bottjer 1997); B: Profile view of microbial mat deformed by intrusion of a gas dome from beneath (modified from Bose and Chafetz 2009); C: Microbial mat chips on Fishermans Island, Virginia (modified from Noffke 2008); D: Demonstration of the flexibility of microbial mats (modified from Cuadrado and Pizani 2007).

Dornbos et al. 2005). The initial colonization of the seafloor by burrowing organisms was stymied by the presence of microbial mats that controlled the euxinic chemistry of the infaunal realm and limited bioturbation to the upper few millimeters of substrate where conditions were more favorable to metazoan activity (Bailey et al. 2006). Burrowing promoted exchange of oxygen between sediments and the overlying water column and mixing of sediments buried or smothered microbial mats; thus, this action continually increased the habitability of the infaunal realm for metazoans while eliminating the microbial competition. By the time of the Cambrian Radiation bioturbation was becoming increasingly common in environments previously dominated by microbial communities (Bailey et al. 2006). Bioturbation became the control on this new, “Phanerozoic”-style substrate: these substrates are soft and soupy, with a well-developed mixed layer, and increased water and oxygen content (Seilacher and Pflüger 1994).

This transition from Proterozoic- to Phanerozoic-style substrates was a geologically rapid, one-way event that occurred within the same timeframe as the Cambrian Radiation, concurrent with the appearance and diversification of burrowing metazoans (Seilacher and Pflüger 1994). Once Phanerozoic-style substrates were introduced into the shallow marine environment, Proterozoic-style substrates were unable to re-establish themselves except under unusual environmental conditions (i.e. end-Ordovician and end-Permian extinctions; Sheehan and Harris 2004; Pruss et al. 2004). Seilacher and Pflüger (1994), recognizing similarities between this event and the

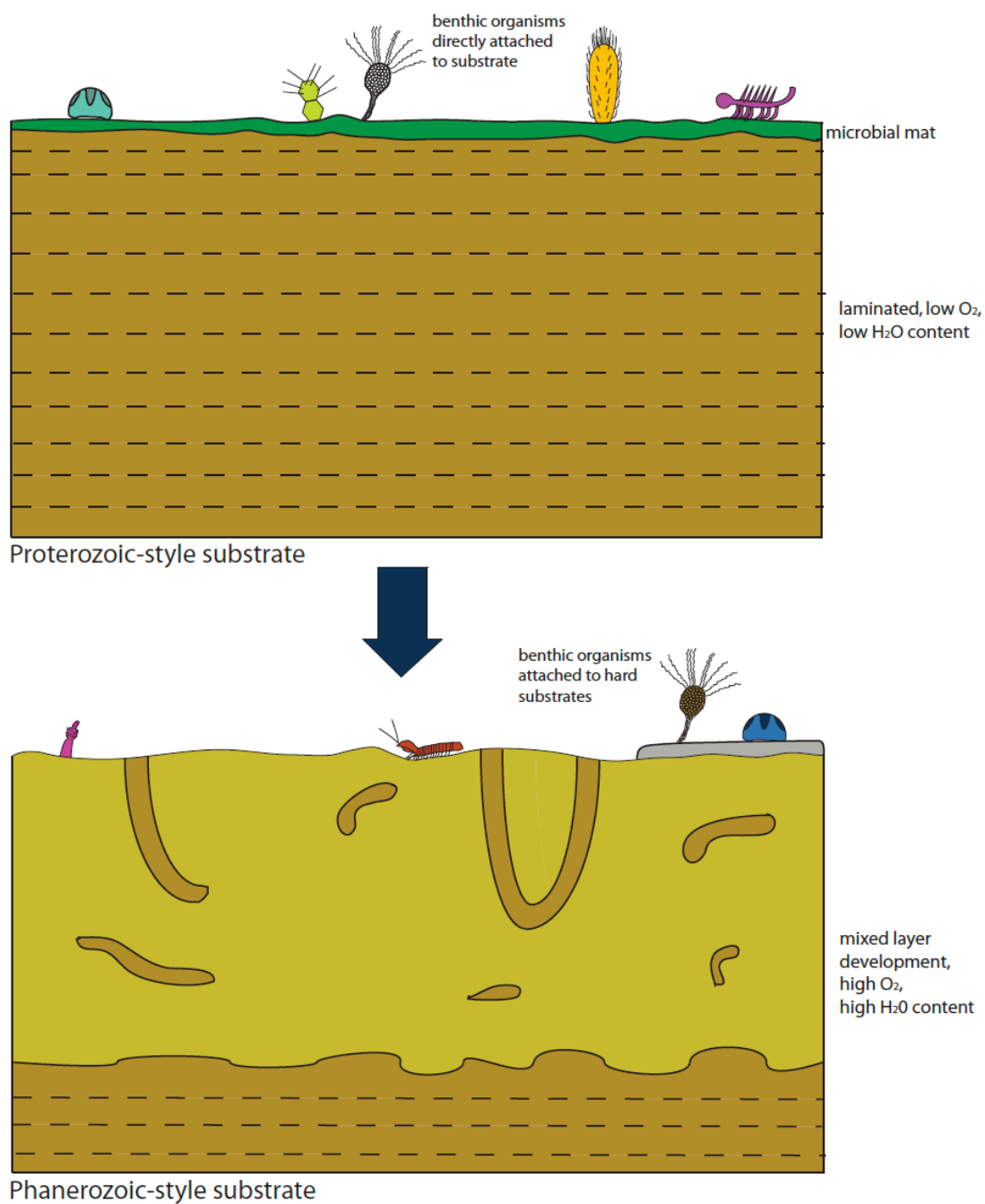


Figure 1.3. Development of marine substrates during the agronomic revolution. Increases in bioturbation across the Proterozoic-Cambrian boundary led to fundamental changes in the nature of marine seafloors, and in turn affected the evolutionary development of benthic and infaunal organisms. effects of agriculture on terrestrial soils, coined the term “agronomic revolution” to describe the Proterozoic-Phanerozoic substrate transition (Fig. 1.3). The agronomic revolution had profound effects on marine environment and marine community ecology.

1.3 The Cambrian Substrate Revolution

The hallmark of the Cambrian Radiation is its residents: namely, many putative metazoans exhibiting very unusual body plans that do not fit neatly into the modern phyla (Gould 1989). Originally thought of as “failed experiments” doomed by a quirk of evolution (Gould 1989), more recent investigations have recognized the significance of changing ecological conditions as driving factors in early animal evolution. Ecological traits universally observed within modern marine communities—predation, biomineralization, and burrowing- were ecological innovations at the time of the Cambrian. As a result Cambrian organisms were the first to adapt to increasing ecological interactions with one another and their environment; and unusual morphologies were one result of these adaptations.

Unusual Cambrian body plans have a strong correlation to the evolution of burrowing organisms, and is evident in early echinoderms (Fig. 1.4) (Bottjer et al. 2000; Parsley and Prokop 2004; Dornbos 2006; Domke and Dornbos 2010), mollusks (Fig. 1.5) (Gehling 1996; Bottjer et al. 2000; Dornbos et al. 2004) and some enigmatic Cambrian groups (Butterfield 1990; Bengtson et al. 2002; Randell et al. 2004; Dornbos et al. 2005; Kloss et al. 2009). These organisms were either immobile benthic metazoans that relied upon marine substrates for attachment and stabilization for survival; or they are mobile

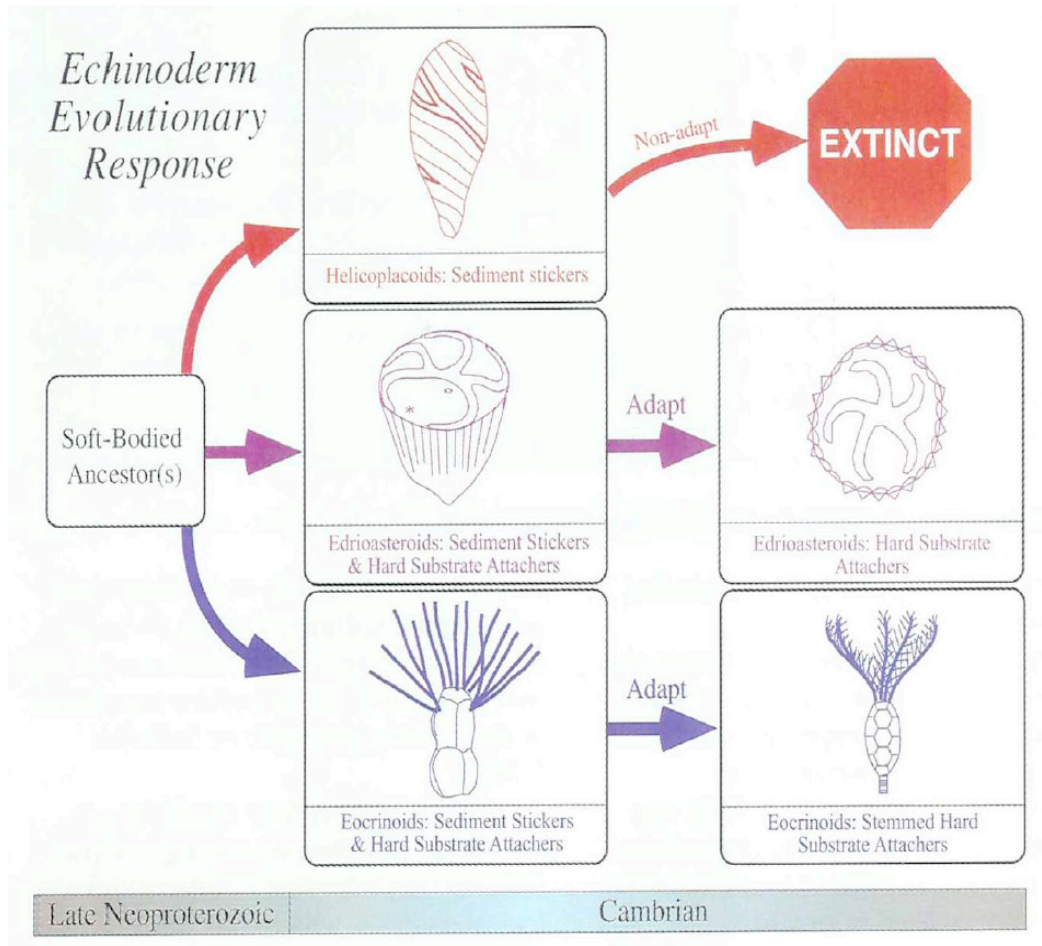


Figure 1.4. The evolutionary responses of early echinoderms to the agronomic revolution. Edrioasteroids and eocrinoids adapted new methods of attachment to substrate by the end of the Cambrian. By comparison, helicoplacoids went extinct due to their inability to adapt to changing substrate conditions. (modified from Bottjer et al. 2000)

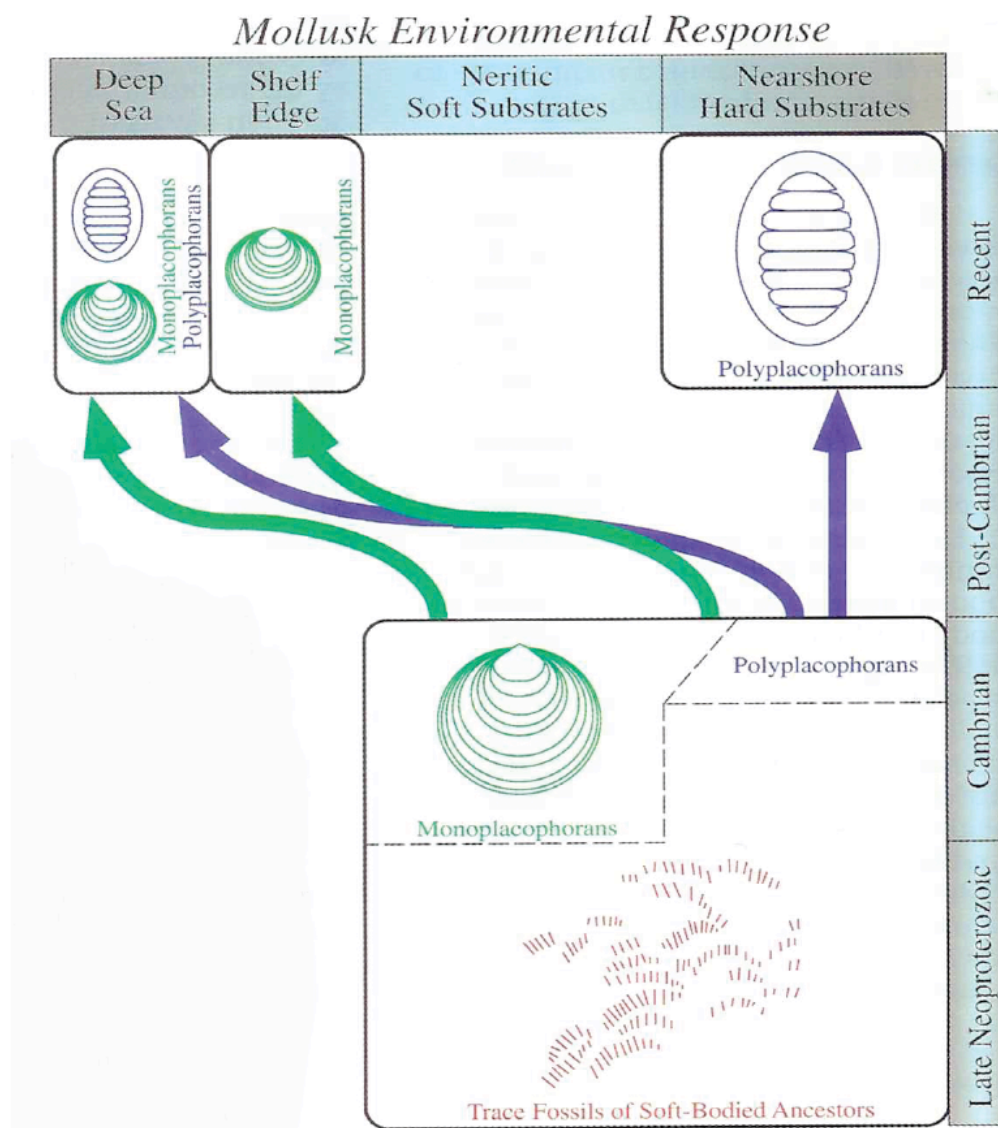


Figure 1.5. Ecological response of early mollusks to the agronomic revolution. The agronomic revolution caused a migration of mats to different environments, and mono- and polyplacophoran followed their food source into new marine environments. (modified from Bottjer et al. 2000)

scavengers/predators that utilize the substrate as a source of food. None were infaunal burrowers; rather, they were profoundly affected by the activities of burrowing organisms.

The agronomic revolution was driven by burrowing organisms; and while a rapid event in the geologic sense, for a period of time during the early-middle Cambrian both Proterozoic- and Phanerozoic-style substrates coexisted in shallow marine setting. The distinctive nature of both substrate styles led to the evolution of two separate and unique “suites” of adaptive strategies designed to maximize the stability of immobile benthic metazoans on the seafloor. Not surprisingly, organisms adapted for living on Proterozoic-style substrates would find it difficult to survive in Phanerozoic-style substrate environments, and vice versa. The agronomic revolution had a predictable affect on Proterozoic-style adapted organisms, fating them to a precipitous decline as their favored substrates disappeared. Immobile benthic metazoans were forced to respond to the agronomic revolution in a series of evolutionary and ecological changes termed the “Cambrian substrate revolution” (CSR) (Bottjer et al. 2000). Immobile benthic metazoans caught up in the CSR faced one of three outcomes:

- 1) Evolving new adaptations to changing substrate conditions. This is evident in a number of early echinoderms, notably the edrioasteroids and eocrinoids that evolved “true” stems for attachment to hard substrates (Bottjer et al. 2000; Domke and Dornbos 2010)

- 2) Relocating to marine environments where Proterozoic-style substrate conditions could still persist. This is observed in the mono- and polyplacophoran mollusks, which are found in shallow subtidal marine settings prior to and during the Cambrian, but thereafter are restricted to deeper marine or nearshore settings where their microbial food sources are not affected by intense bioturbation (Bottjer et al. 2000)
- 3) Extinction. The helicoplacoid echinoderms and cancelloriids are temporally restricted to the Cambrian and their extinction is roughly coincident with the end of the agronomic revolution (Dornbos and Bottjer 2000). Both groups exhibit similar adaptive strategies and morphologies, and it is possible that certain Proterozoic morphologies were unable to successfully adapt to changing seafloor conditions (Kloss et al. 2009).

The CSR radically alters the perception of “unusual” body plans: once thought of as early experiments in animal evolution, we now understand that these animal morphologies were successful adaptations to nonactualistic substrate conditions that we cannot hope to identify within modern marine settings. These Cambrian metazoans were not failures, rather they were specialists adapted to shrinking seafloor habitats.

1.4 Burgess-Shale-type preservation and its relationship to the agronomic and Cambrian substrate revolutions

The exquisite nature of preservation displayed among many Cambrian fossil Konservat Lagerstätten has provided a high fidelity view into the marine communities present at this critical period in evolutionary history. While examples of exceptional fossil preservation are known from many periods throughout geologic history (Bottjer et al. 2002), the Neoproterozoic-Phanerozoic transitional period harbors a disproportionate number of Lagerstätten for reasons that are still not exactly clear. The reasons behind their abundance are nearly as tantalizing as the abrupt closing of this “taphonomic window” by the late Cambrian period.

Soft-bodied preservation—preservation of non-biomineralizing biologic structures—takes on a variety of taphonomic forms during the Neoproterozoic-Phanerozoic transition (Butterfield 2003) but Burgess-Shale-type (BST) preservation is most commonly encountered in Cambrian shales. BST fossils are preserved as carbonaceous compressions, their three-dimensional structures flattened as a consequence of the collapse of supporting soft tissues (Butterfield 2003), and shows a taphonomic bias towards non-biomineralizing extracellular structures: cuticle, chaetae, and jaws (Briggs and Kear 1993). The “holotype” for BST preservation is its namesake, the Burgess Shale (British Columbia), although this method of preservation is also found in the Maotianshan Shale (Chengjiang Fauna, China), Emu Bay Shale (Australia), Kinzers Formation (Pennsylvania, USA), Marjum Formation and Wheeler Shale (Utah, USA), Indian Springs Lagerstätte (Nevada, USA), and Spence Shale (Idaho/Utah, USA) (Robison 1991; Dornbos et al. 2005; Powell 2009; English and Babcock 2011; Hall et al. 2011).

Examples of BST faunas are observed from the Neoproterozoic to the middle Cambrian (Butterfield 1995), but it ceases to exist by the late Cambrian (Butterfield 2003).

Multiple attempts have been made to explain BST preservation, and current hypotheses focus on small-scale geochemical pathways (Butterfield 1990, 1995; Orr et al. 1998; Petrovich 2001; Gaines et al. 2005; Gaines et al. 2012). All of these mechanisms operate under dysoxic or anoxic conditions (Gaines and Droser 2010). Most BST faunas are traditionally interpreted as having been transported from oxygen-rich habitable localities into oxygen-poor burial zones (Conway Morris 1986; Butterfield 1990; Gaines et al. 2005), where anoxic conditions can serve as a medium for geochemical processes to take place as well as a barrier to biologically-induced decay. While trace fossils are occasionally associated with BST faunas (Lin et al. 2010), the majority of BST fossils are preserved in strata where bioturbation is absent (Gaines and Droser 2010). Recent geochemical studies have suggested that shales preserving BST faunas are associated either with a continually oxic water column (Powell 2009; Hall et al. 2011) or a water column that fluctuated between periods of oxic and anoxic conditions (Handle and Powell 2010), implying that anoxia may be overemphasized as a prerequisite for BST preservation.

1.5 The agronomic revolution, the CSR, and geochemical analysis of Cambrian substrates

Paleoecological studies that utilize connections between substrate conditions and the adaptations of benthic fauna are based upon the association between fossils and the rocks in which they are preserved (i.e. Dornbos et al. 2005; Domke and Dornbos 2010). Thus, the connection comes with a caveat: if fossil specimens are not preserved *in situ*, then sedimentological data related to bioturbation is useless. This is a challenge in light of studies that suggest dissolved oxygen concentrations (DOC) were too low in marine bottom waters to support an *in situ* benthic fauna in some Cambrian environments (Gaines and Droser 2003; Garson et al. 2008) and current hypotheses to explain the preservation of the fossils themselves (Butterfield 1990, Petrovich 2001, Gaines et al. 2005).

Sedimentological studies like Gaines and Droser (2003) and Garson et al. (2008) utilize trace fossil proxy models, developed using recent marine settings that are dominated by Phanerozoic-style substrates to approximate bottom water oxygenation (Fig. 1.6) (Savrda and Bottjer 1987; Ekdale 1988). It should be clarified that these studies are not necessarily relying upon the ichnofacies presented in these models for comparisons; but rather, they are making the same interpretations of unbioturbated substrates (“no ichnia”; Ekdale and Mason 1988) presented in these models: a lack of bioturbation indicates a lack of oxygenation in the marine environment. The difficulty in

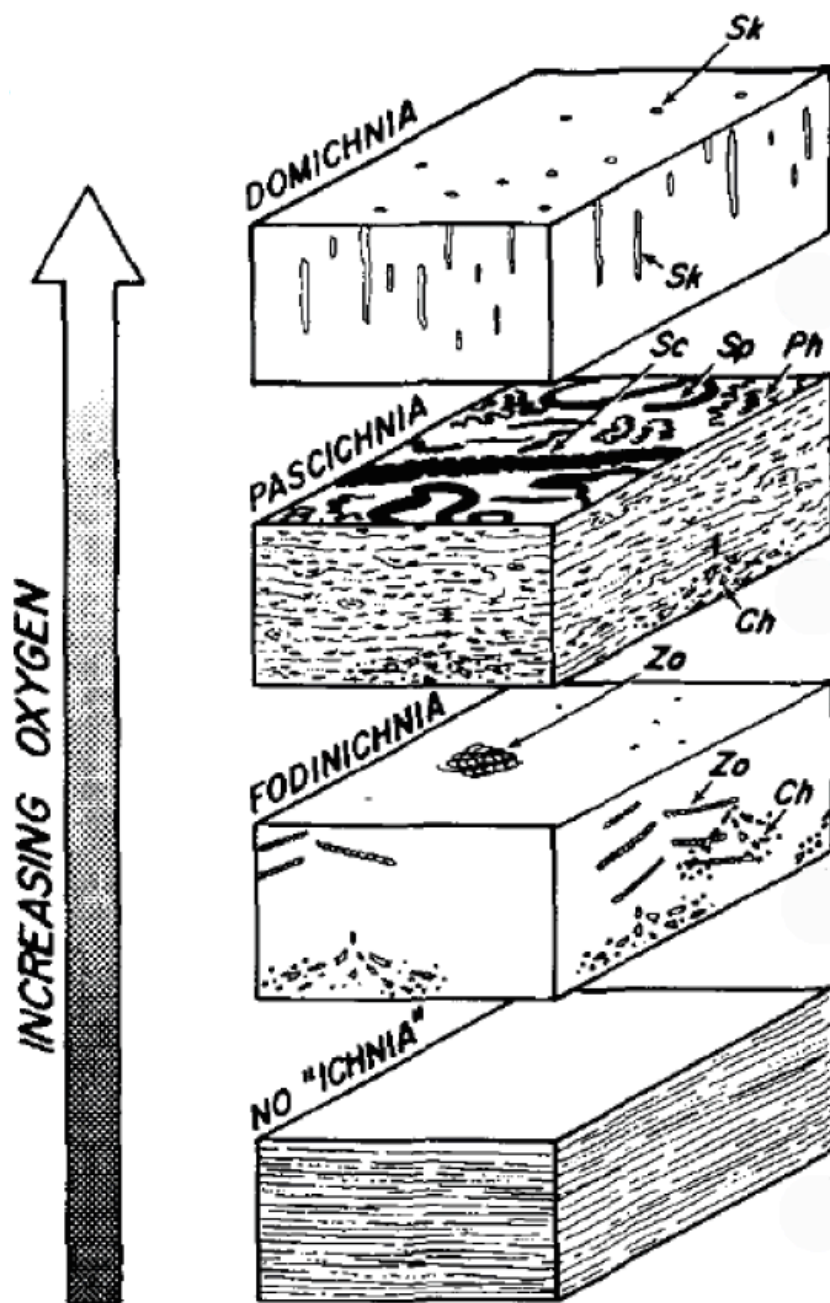


Figure 1.6. One model to describe changes in ichnofacies as a function of bottom water oxygenation. As dissolved oxygen concentration (DOC) increases so does the diversity and complexity of trace fossils. A lack of DOC in the marine environment is typically associated with a lack of tracemaking behavior, i.e. "no ichnia." This model was based upon trace-fossil-rich strata from the Oquirrh Basin, Utah, which is dated to the Carboniferous-Permian. Phanerozoic-style substrates were ubiquitous during this time. (modified from Ekdale and Mason 1988)

using these models for Cambrian environments is that they do not adequately describe substrates where environmental or ecological conditions are unique and atypical: for example, when burrowing organisms can tolerate anoxic near anoxic settings (Levin et al. 2003). Thus, these interpretations could pose problems in light of the agronomic revolution and the CSR: these events indicate that non-actualistic conditions persisted in Cambrian substrates for some time after the initiation of bioturbation. Since non-actualistic conditions by definition are not observed in later Phanerozoic to modern shallow seafloor environments, these ichnofacies models may not accurately reconstruct paleoredox conditions during the Cambrian Radiation.

At the same time the interpreted methods of fossil preservation for faunas associated with the Spence and Wheeler Shale present similar difficulties for paleoecological studies. If BST preservation requires that faunal assemblages be transported into anoxic environments prior to burial (Conway Morris 1986; Gaines et al. 2005), then paleoecological studies fails for a number of reasons: 1) faunal assemblages do not represent true, living marine communities but instead an assorted collection of communities brought together through burial; 2) fauna were likely transported from local environments near the oxic-anoxic boundary, an ecologically stressful environment that is not indicative of normal marine communities (Gaines and Droser 2010); 3) comparisons between sedimentology, ichnology, and faunal assemblages are not ecologically informative. The work of Caron and Jackson (2006), Schlottke (2008), Kloss et al. (2009), and Powell (2009) have suggested that at least portions of BST faunas are

preserved *in situ*, an interpretation that would require reassessment of current taphonomic models to account for these in-place benthic communities.

On one hand there exist paleoecological studies indicating *in situ* preservation of fauna (Zhou and Chen 1997; Caron and Jackson 2006; Kloss et al. 2009), and all the implications thereof for the agronomic and Cambrian substrate revolutions, and on the other hand there are ichnological and taphonomic analyses suggesting that these same fauna were likely not preserved *in-situ* (Rees 1986; Gaines and Droser 2005; Brett et al. 2009). What, then, can be done to reconcile these disparate views?

The solution proposed here is to utilize a multidisciplinary approach to determine the true nature of the relationship between fauna, substrate, and redox conditions in order to determine the distribution of Proterozoic- versus Phanerozoic-style substrate conditions through the Cambrian. The focus of this study is the early-to-middle Cambrian Wheeler and Spence Shales of Idaho and Utah, USA and the Maotianshan Shale of China, and their associated faunas. Substrate conditions were evaluated through ichnofabric analysis to determine the relative dominance of substrate style in comparison to other known Cambrian localities. A comparison with trace fossil model proxies was also made. Morphological diversity among benthic communities was analyzed to determine their fitness relative to substrate conditions, including a discussion on morphological adaptations and comparisons with ichnofabric data. Finally, geochemical analyses via X-ray fluorescence (XRF) was utilized to assess the likelihood of bottom water oxygenation in these environments, and compared with the ichnological

and paleoecological data sets to understand the overall paleoenvironmental conditions present in the Wheeler and Spence Shales. The goal of this approach is to test the hypothesis that DOC concentrations were high enough in the marine bottom waters of early-middle Cambrian shales to support the presence of a benthic infauna, despite a lack of observable intense bioturbation. Under this hypothesis, many Cambrian seafloor settings had low levels of bioturbation because animals had not adapted sufficiently to burrow into the full spectrum of normal marine seafloor sediments, not because of low oxygen levels. If this hypothesis is supported, then this study would provide strong evidence for the CSR and demonstrate the utility of geochemical analyses for environments where non-actualistic environments are suspected but cannot be definitively determined from sedimentological or paleoecological studies alone.

CHAPTER 2: BIOTURBATION AND SUBSTRATE CONDITIONS

The presence or absence of bioturbation is a major control on the development of substrate conditions during the agronomic revolution (see Section 1.2). Therefore, by measuring the relative amount of bioturbation in Cambrian shales, one can determine whether Proterozoic- or Phanerozoic-style substrates were present in the benthic environment. Studies of Cambrian shales often utilize ichnofabric analysis for interpretations of redox rather than substrate conditions (e.g. Rees 1986, Gaines and Droser 2003, Brett et al. 2009, Garson et al. 2012), based upon observations of normal marine Phanerozoic settings (Savrda and Bottjer 1986, Ekdale 1988). Ichnological and sedimentological analysis is carried out on the three aforementioned Cambrian shales (see Chapter 1) in order to determine the dominant substrate conditions present at the time of deposition. All three Cambrian shales consistently demonstrate a lack of bioturbation, which is suggestive of the presence of Proterozoic-style substrates. This interpretation is supported by the preservation of cohesive sedimentary structures associated with unbioturbated laminations, which are suggestive of the presence of microbial mats. The presence of Proterozoic-style substrates are expected in Cambrian marine substrates due to the agronomic revolution, and the unique transitional substrate environment created by the revolution limits the utility of ichnofacies models in interpreting redox conditions for Cambrian paleoenvironments.

2.1 Controls on Marine Substrate Conditions

The term substrate refers to any medium that exists on the seafloor bottom. The “condition,” “character,” or “style” of substrate refers to a unique combination of physical, chemical, and biological factors that define the nature of, and determines the extent of interaction organisms have with, said substrate (Fig. 2.1). Substrate conditions are critical to the survival of immobile benthic metazoans—organisms that rely upon life-long consistency in substrate for successful attachment and stabilization upon the seafloor (Bottjer et al. 2000). Substrate conditions remained relatively uniform in shallow subtidal marine settings through the majority of the rock record, with the Proterozoic- and Phanerozoic-style substrates dominating their respective periods of geologic time, with a short transitional period at the Neoproterozoic-Phanerozoic boundary and continuing into the late Cambrian when both substrate styles coexisted on a heterogeneous seafloor. This transitional event, the agronomic revolution, was in part responsible for the evolutionary changes resulting in the morphologies of modern immobile benthic metazoans (Seilacher and Pflüger 1994; Bottjer et al. 2000).

The agronomic revolution itself was driven by the activities of infaunal burrowers (Seilacher and Pflüger 1994). Burrowing is first observed in the Ediacaran, sometimes in association with the Ediacaran fauna but likely created by the feeding and locomotive habits of early bilaterians (Narbonne 1998; Jensen et al. 2005; Seilacher et al. 2005; Buatois and Mangano 2011). These first burrowing traces are extremely shallow, penetrating only a few millimeters beneath the substrate, oriented parallel to the

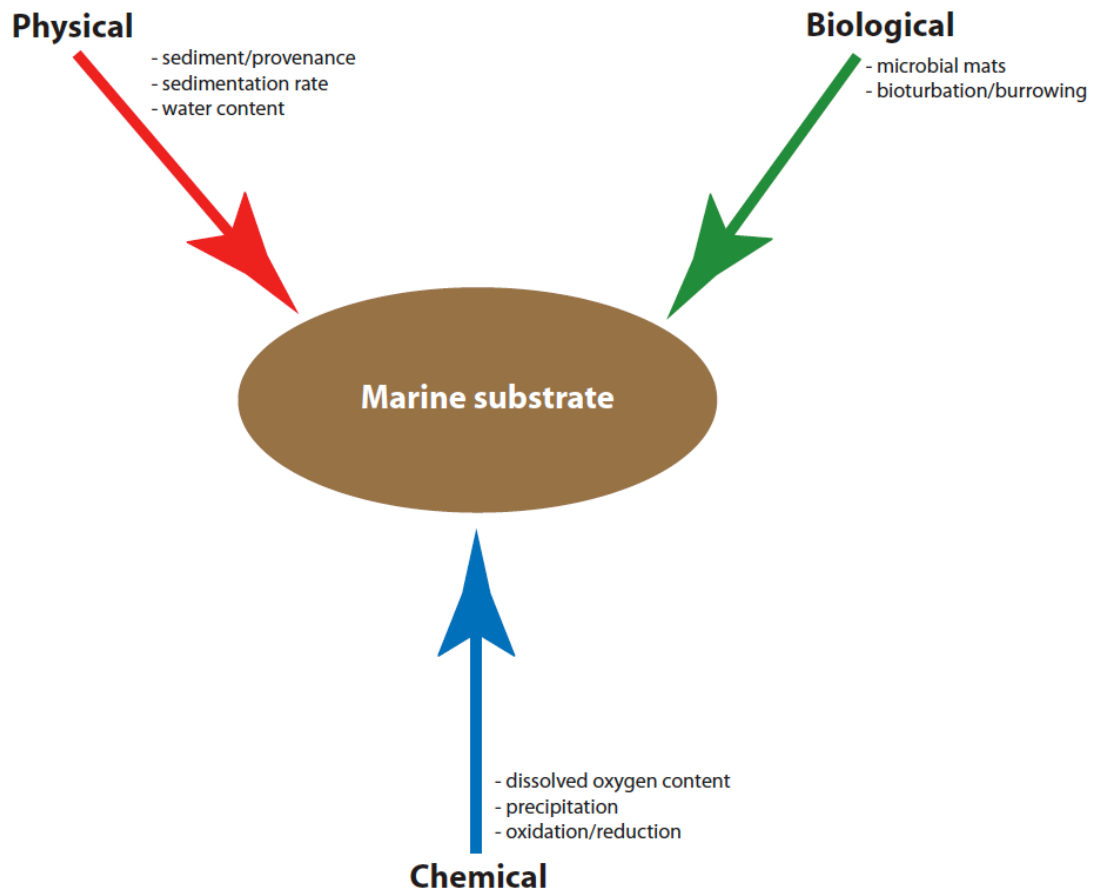


Figure 2.1. Illustration demonstrating the physical, biological, and chemical factors involved in the development of marine substrates.

bedding surface, and are found in unison with organosedimentary structures interpreted as microbial mat features suggesting that this style of burrowing did not negatively impact the growth of microbial communities (Fig. 2.2) (Seilacher et al. 2005; Buatois and Mangano 2011). Burrowing behaviors grew increasingly complex during the Cambrian: burrowing traces became increasingly meandering, penetrating to greater depths and oriented generally perpendicular to the bedding plane (Fig. 2.2) (Buatois and Mangano 2003; Seilacher et al. 2005). This change in burrowing complexity was likely an effect of the broader Cambrian Radiation: evolutionary pressure from predation and competition for resources drove the development of more penetrating burrowing styles in search of food and shelter. This more aggressive burrowing style altered the physical and chemical nature of substrates in numerous ways: it thoroughly mixed and homogenized sedimentary material, it blurred the contact between the sediment surface and overlying water column, and it delivered increasing volumes of water and dissolved oxygen into the infaunal realm (Seilacher and Pflüger 1994).

Such changes proved disastrous for microbial communities inhabiting these substrates who were unable to compete with burrowing organisms. Microbial communities, formerly the controlling factor in the development of Proterozoic-style substrates, slowly gave way to the influence of burrowing metazoans and their modified Phanerozoic-style substrates. By the end of the Cambrian the revolution was over and mobile organisms won; Phanerozoic-style substrates would dominate shallow subtidal marine settings from the end Cambrian until today, and immobile benthic metazoans would need to evolve adaptive strategies to cope with the presence of these sediments.

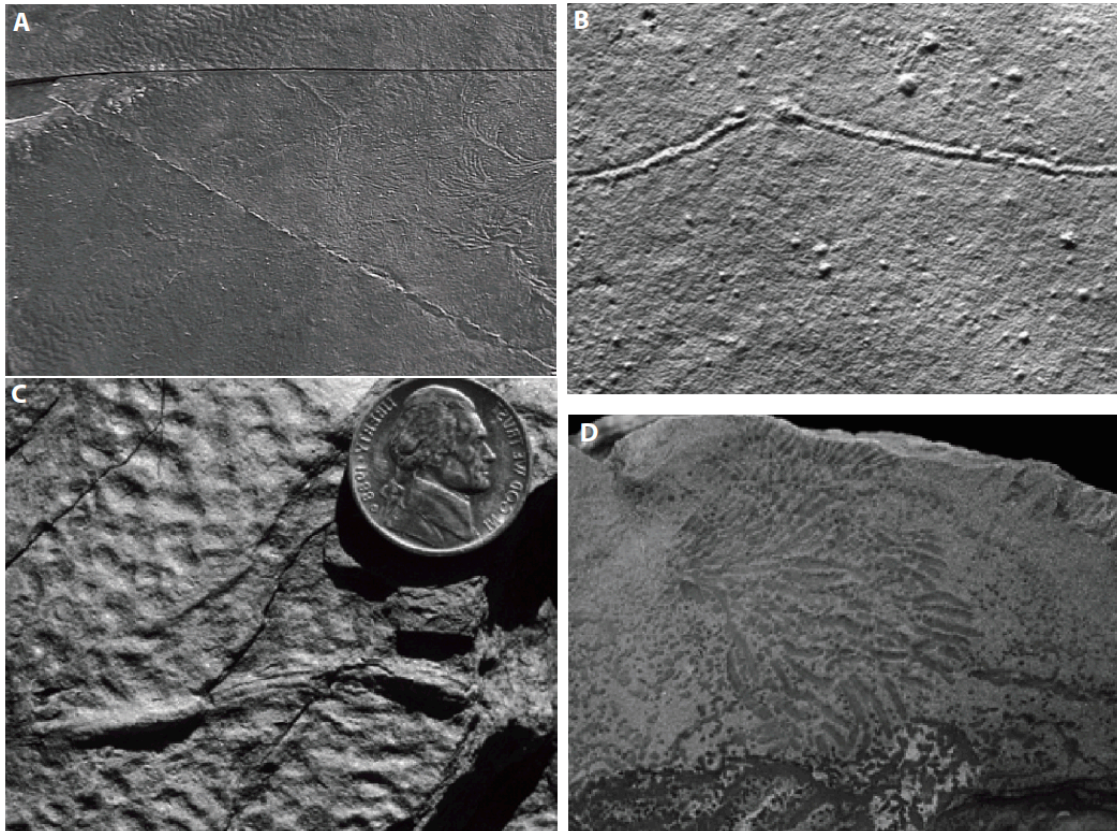


Figure 2.2. Trace fossils typical of the Neoproterozoic-Early Cambrian. A: *Oldhamia alata* (right) preserved in association with putative microbial mat structures (upper and lower left), early Cambrian Puncoviscana Formation, Argentina (modified from Buatois and Mangano 2012); B: horizontal trace fossil burrow, Ediacaran Tucuari Formation, Uruguay (modified from Pecoits et al. 2012); C: back-filled trace fossil preserved in association with microbial mat structures, early Cambrian Harkless Formation, California USA (modified from Gingras et al. 2011); D: *Oldhamia* (?) trace fossil preserved on the sole bed beneath mat laminations, Ediacaran Rawnsley Quartzite, Australia (modified from Gingras et al. 2011).

2.2 Quantitative Measures of Bioturbation

Truly quantitative measurements of burrowing intensity are difficult to obtain, and most analyses of burrowing and trace fossils use either qualitative and or semi-quantitative approaches, and both have been used to evaluate the paleoenvironmental context of Neoproterozoic-Cambrian substrates. Trace fossil models like those developed by Savrda and Bottjer (1987) and Ekdale (1988) are qualitative in nature and utilize observed associations between ichnofossils to evaluate relative concentrations of dissolved oxygen (DOC) present in the benthic marine environment. The models were based on observations of modern trace fossils in variable aerobic environments and case studies from the geologic record, and have been used extensively for paleoenvironmental interpretations in Phanerozoic units (see Leszczynski et al. 1996; Raiswell et al. 2001; Algeo and Maynard 2004; Boyar and Droser 2011; Rodriguez-Tovar and Uchman 2011). Similar methodologies are utilized by workers Gaines and Droser (2003), Garson et al. (2008) Brett et al. (2009) for interpretations of Cambrian shales. A second approach to analyzing bioturbation is through the semi-quantitative method of ichnofabric indexing (ii), first developed by Droser and Bottjer (1986). Here the relative intensity of bioturbation is visually observed as a fraction of sedimentary material disturbed by burrowing activity, and is graded on a simple scale: ii1- no bioturbation present, primary sedimentary fabrics preserved intact; ii2- >20% sediment disturbed by bioturbation, primary sedimentary fabrics intact; ii3- >50% sediment disturbed by bioturbation, few primary sedimentary fabrics intact; ii4- >80% sediment disturbed by bioturbation, primary sedimentary fabrics destroyed; ii5- complete homogenization of

sediment by bioturbation, primary sedimentary fabrics completely destroyed (Fig. 2.3) (Droser and Bottjer 1986). The ii-method was designed specifically for use with Cambrian-age siliciclastic sediments where descriptions of biologically mediated sedimentary fabrics were difficult—within the transitional period between unbioturbated Proterozoic-style substrates and later bioturbated Phanerozoic-style substrates (Droser and Bottjer 1986). The ii-method straddles the gap between the two substrate end members, and thus can be used as a yardstick to gauge the relative dominance of Proterozoic- (ii-1) versus Phanerozoic- (ii-5) style substrates, and as such has been extensively applied to numerous studies of Cambrian benthic faunas (Bottjer et al. 2000; Dornbos and Bottjer 2000, 2001; Parsley and Prokop 2004; Kloss et al. 2009; Domke and Dornbos 2010; English and Babcock 2010).

Ichnofabric indices is the preferred method utilized here for analysis of sedimentary fabrics and relative burrowing intensity in the Spence and Wheeler Shales of Utah and Idaho, as the ii-method was developed specifically for fine-grained siliciclastic Cambrian sediments like those of the Spence and Wheeler. Both the Spence and Wheeler Shales are associated with Burgess-Shale-type (BST) Lagerstätten with exceptional soft-bodied preservation of benthic fauna that was likely affected by the Cambrian substrate revolution. In order to better understand how these two BST-faunas were affected by changing substrate conditions, an assessment of relative bioturbation levels was performed to determine the relative substrate conditions present in the Spence and Wheeler Shales at the time of deposition. Since the shales are of early-

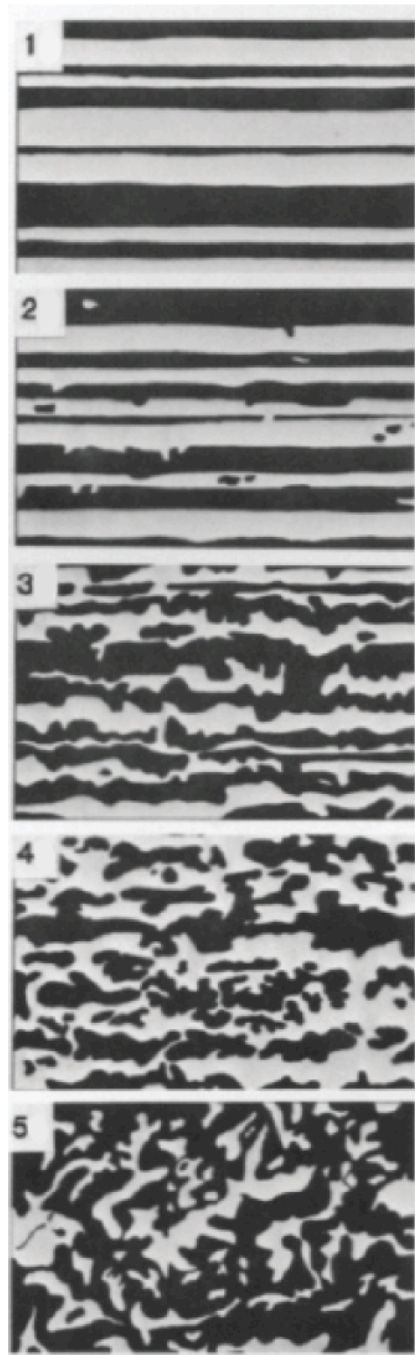


Figure 2.3. The semi-quantitative ichnofabric (ii) index of Droser and Bottjer (1986). 1: No bioturbation, original sedimentary fabrics preserved intact.; 2: Slight disturbance (up to 10% of total) of sedimentary fabrics; 3: Moderate disturbance (10-40%) of sedimentary fabrics, some primary bedding structures destroyed; 4: significant (40-60%) disturbance of sedimentary fabrics, many primary bedding structures destroyed; 5: total homogenization of sediment, complete destruction of primary bedding structures. (modified from Droser and Bottjer 1986).

were affected by changing substrate conditions, an assessment of relative bioturbation levels was performed to determine the relative substrate conditions present in the Spence and Wheeler Shales at the time of deposition. Since the shales are of early-middle Cambrian age, it is hypothesized that the Spence, Wheeler, and Maotianshan Shales will likely exhibit characteristics consistent with transitional substrates: shales will exhibit a combination of layers consisting of extremely low bioturbation consistent with the presence of Proterozoic-style substrates as well as intensively bioturbated layers consistent with the presence of Phanerozoic-style substrates.

2.3 Geologic Setting

2.3.1 The Spence Shale: The middle Cambrian Spence Shale of southern Idaho-northern Utah is the middle member of the Langston Formation, overlying the Naomi Peak Limestone and underlying the High Creek Limestone (Fig. 2.4; Liddell et al. 1997). The Langston Formation was deposited on a carbonate ramp, with the Naomi and High Creek limestones representing deposition along the outer margin of a carbonate belt, and the Spence Shale occupying deposition along a distal portion of the ramp in the outer detrital belt (Fig. 2.4; Liddell et al. 1997). Analysis of sub-centimeter-scale trace fossils from the Spence Shale suggests fluctuations in bottom water oxygenation, which restricted the development of bioturbation but supported a rather diverse dysoxic benthic community (Garson et al. 2008). The Spence Shale is known from a number of

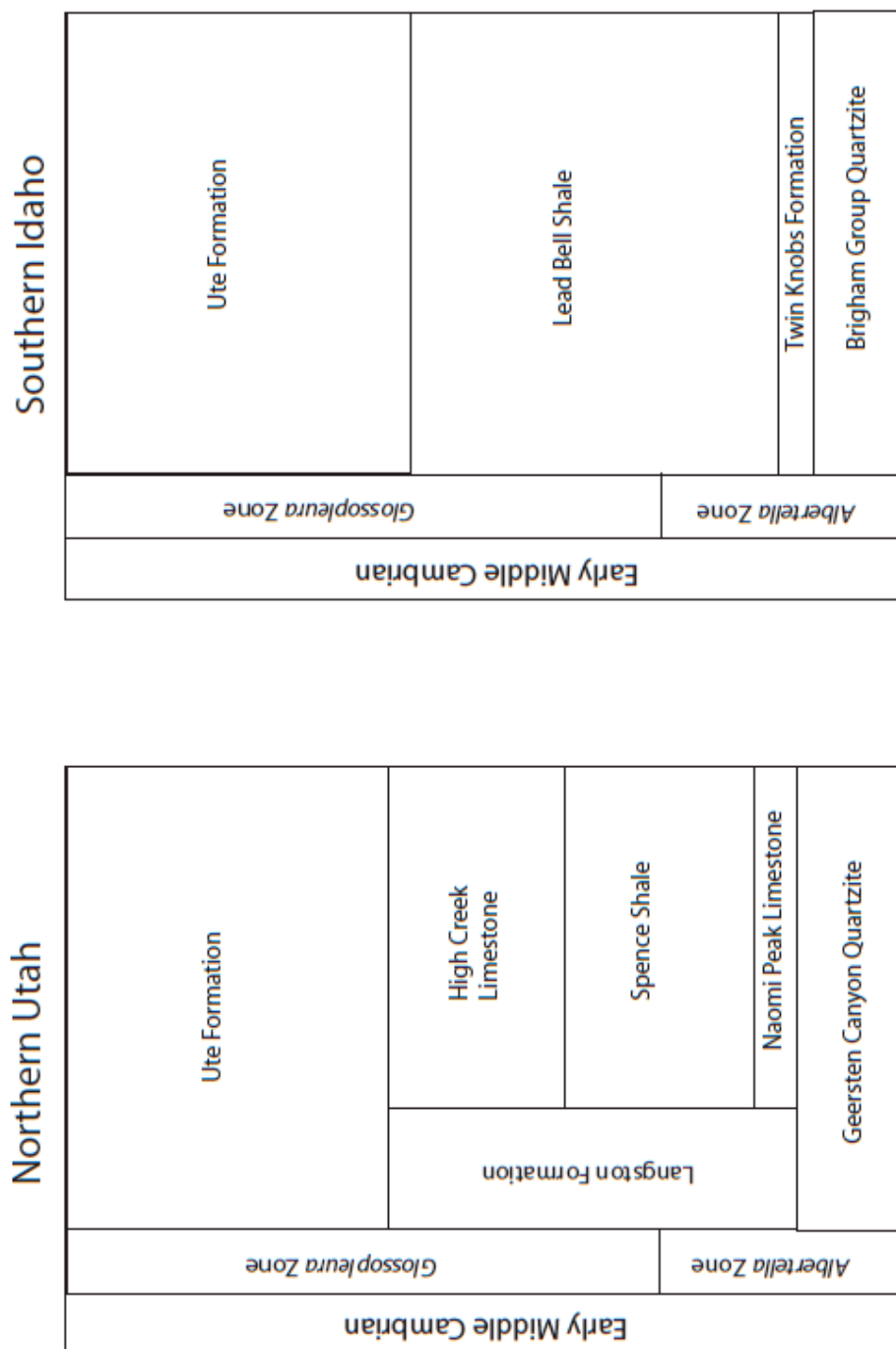


Figure 2.4. Generalized stratigraphy of the Langston Formation and equivalent units in northern Utah and southern Idaho (see Figure 2.6 for locality data). Modified from Liddell et al. (1997).

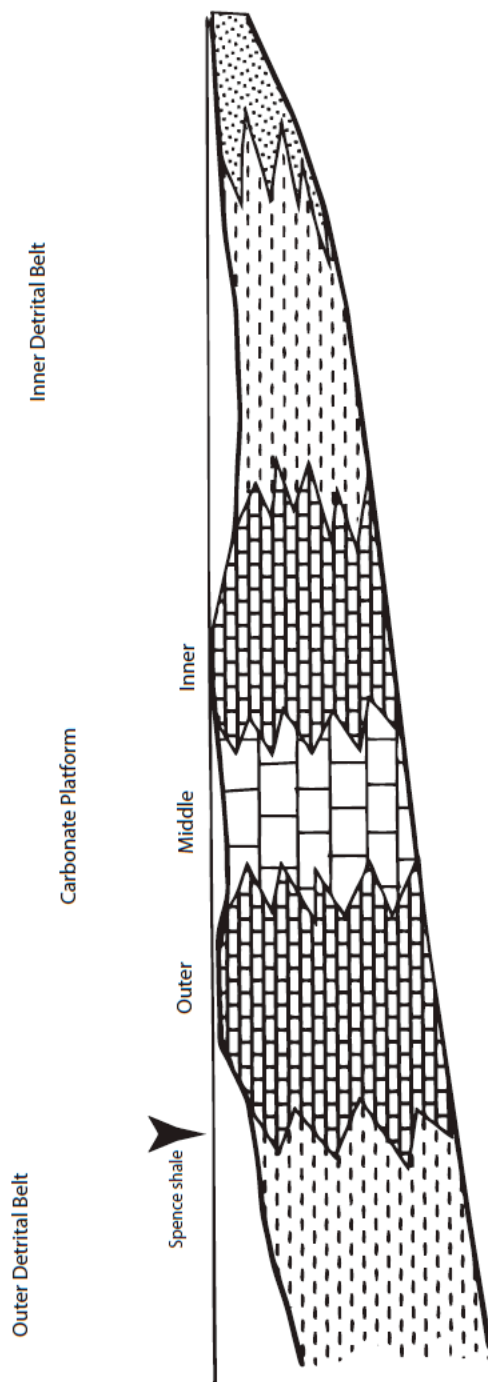


Figure 2.5. Generalized depositional setting of the western Cordillera (i.e. North America) during the Middle Cambrian. The Spence Shale Member of the Langston Formation was likely located near the transitional boundary between the outer detrital belt and the outer carbonate platform (arrow). Figure is modified from Liddell et al. (1997).

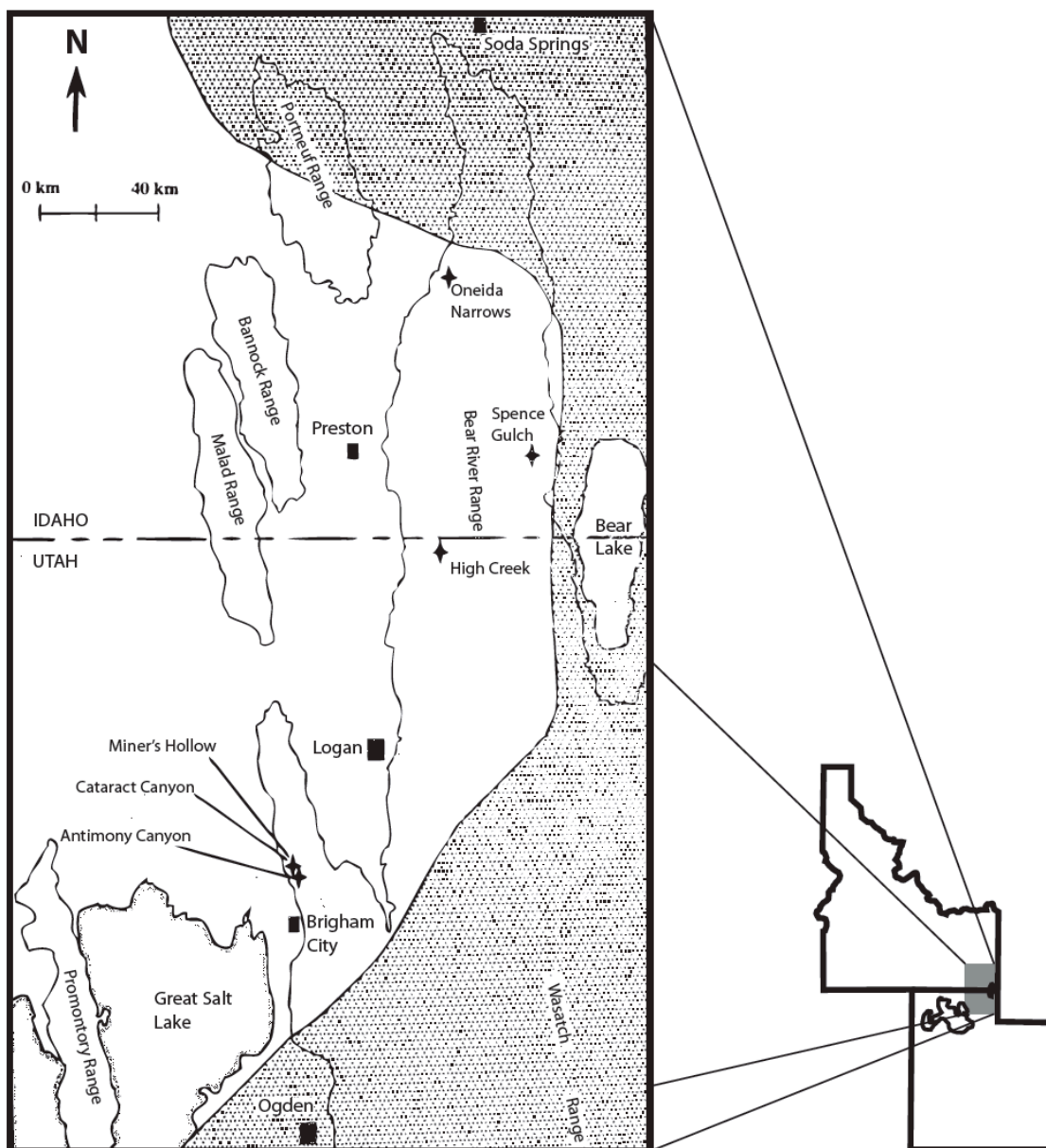


Figure 2.6. Map of Spence shale localities in northern Utah-southern Idaho. Samples collected from four localities-- Miner's Hollow, Oneida Narrows, Spence Gulch, and High Creek-- were utilized for this study. Miner's Hollow provided the largest, best exposed outcrop among the four studied localities. Inset map is modified from Liddell et al. (1997).

localities spanning a distance of approximately 90 miles from near Preston, ID to Brigham City, UT (Fig. 2.5; Liddell et al. 1997). The Spence Shale thickens northward; the Antimony Canyon locality represents the shallowest deposition of the Spence, with Miner's Hollow and Oneida Narrows representing deeper, more offshore settings (Lyon 2011). Liddell et al. (1997) identified seven parasequence sets (Fig. 2.7), each a shallowing upward sequence transitioning from fine-grained shales to a carbonate cap, and distinguishable based upon changes in diversity, size, and taphonomic grade of trilobites. The Spence Shale contains a BST fauna that includes trilobites, arachnomorph arthropods, articulate and inarticulate brachiopods, eocrinoids, edrioasteroids, hyolithids, and sponges (Gunther and Gunther 1981; Robison 1991; Liddell et al. 1997; Church et al. 1999; Sprinkle and Desmond 2006; Briggs et al. 2008; Sprinkle et al. 2009), as well as an uncommon soft-bodied fauna including chancelloriids, anomalocaridids and other arthropods, wiwaxiids, annelids, and algae (Robison 1969; Briggs and Robison 1984; Conway Morris and Robison 1988; Robison 1991; Briggs et al. 2008).

2.3.2 The Wheeler Shale: First named by Charles D. Walcott (1908) due to its location within the Wheeler Amphitheatre (Fig. 2.8), the middle Cambrian Wheeler Shale of central Utah is bounded below by the Swasey Limestone and above by the Marjum Formation (Fig. 2.9) (Rigby 1978). The shale was deposited in a subtropical-to-tropical setting, 15-20 degrees north of the equator (Scotese 1997), within a fault-controlled trough that developed during the middle Cambrian known as the House Range Embayment (Fig. 2.10) (Rees 1986). Prior to the development of the House Range embayment

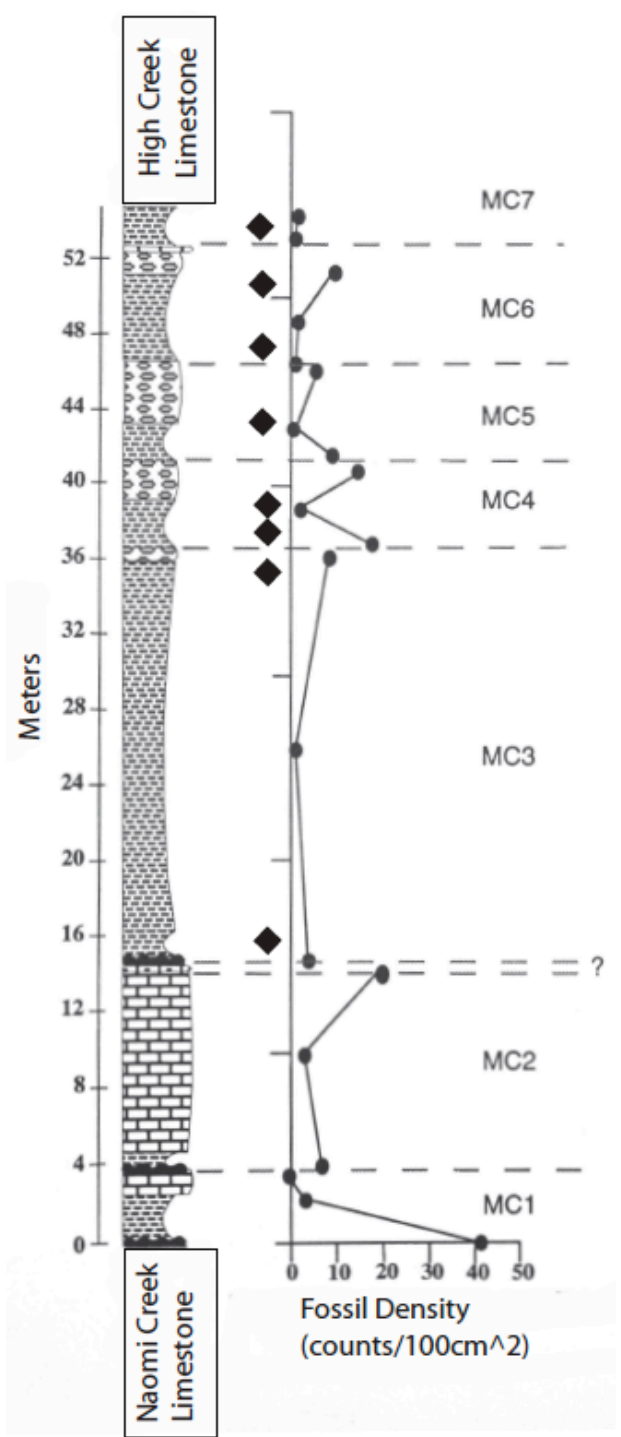


Figure 2.7. Stratigraphy of Spence Shale at Miner's Hollow and fossil densities observed per parasequence (modified from Liddell et al. 1997). Note how fossil density is greatest at bottom and top of parasequences. Black diamonds indicate stratigraphic intervals sampled for ichnofabric and geochemical analysis in this study.

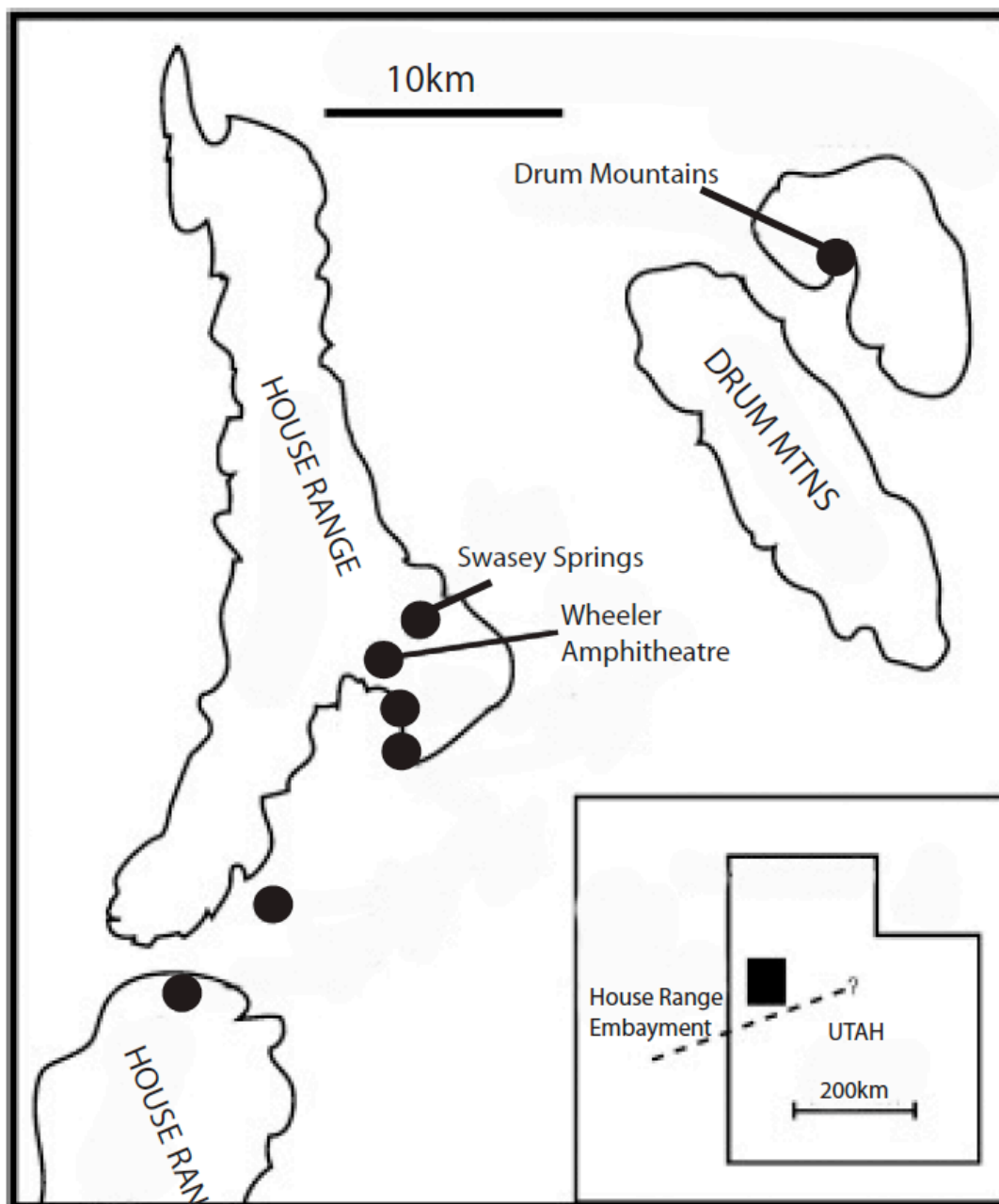


Figure 2.8. Map of Utah showing locations of Wheeler shale (black dots). Samples utilized in this study were collected from the Wheeler Amphitheatre. Modified from Gaines and Droser (2010).

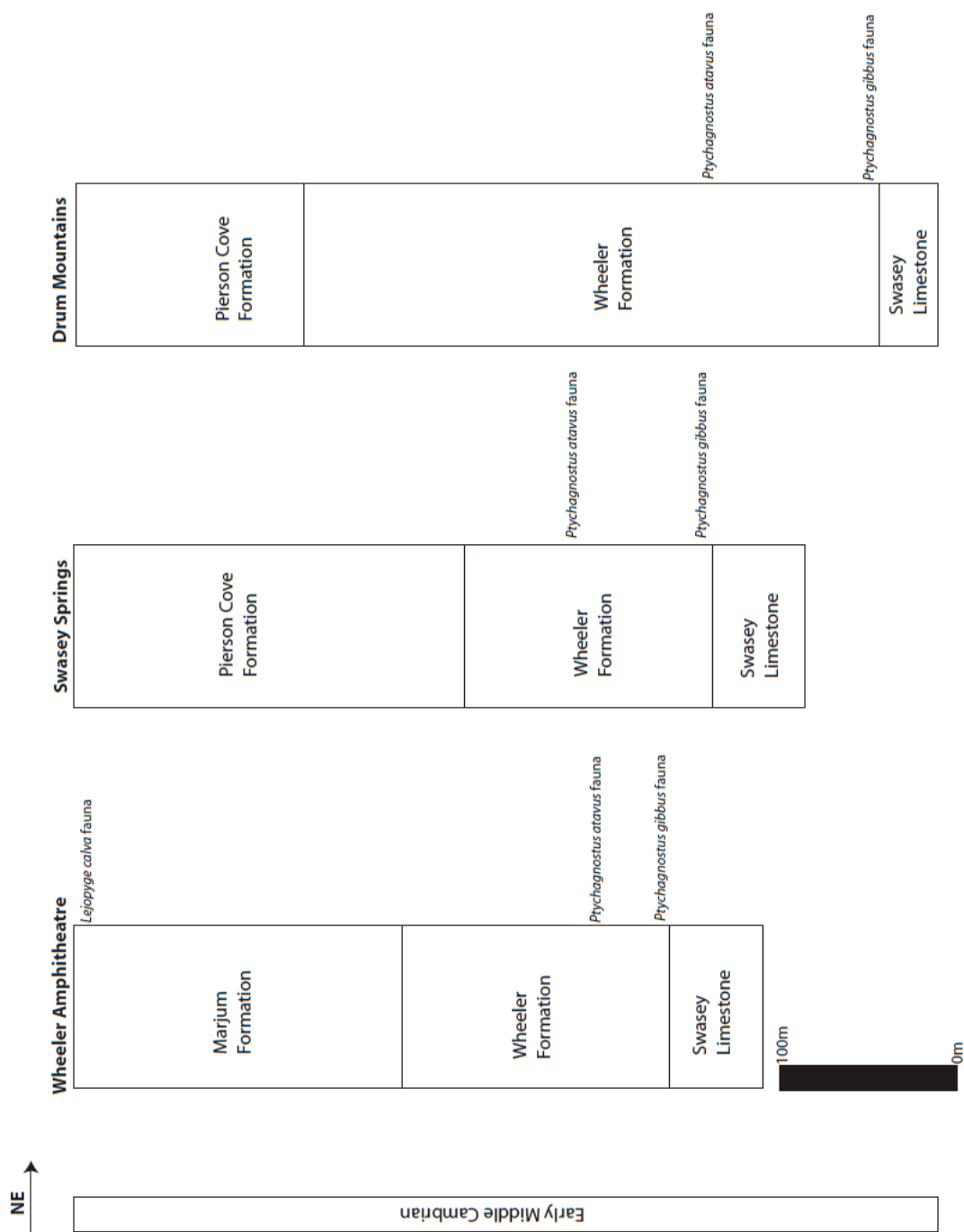


Figure 2.9. General stratigraphy of the Wheeler Formation and associated units in Utah (see Figure 2.8 for locality data), after Rees (1986).

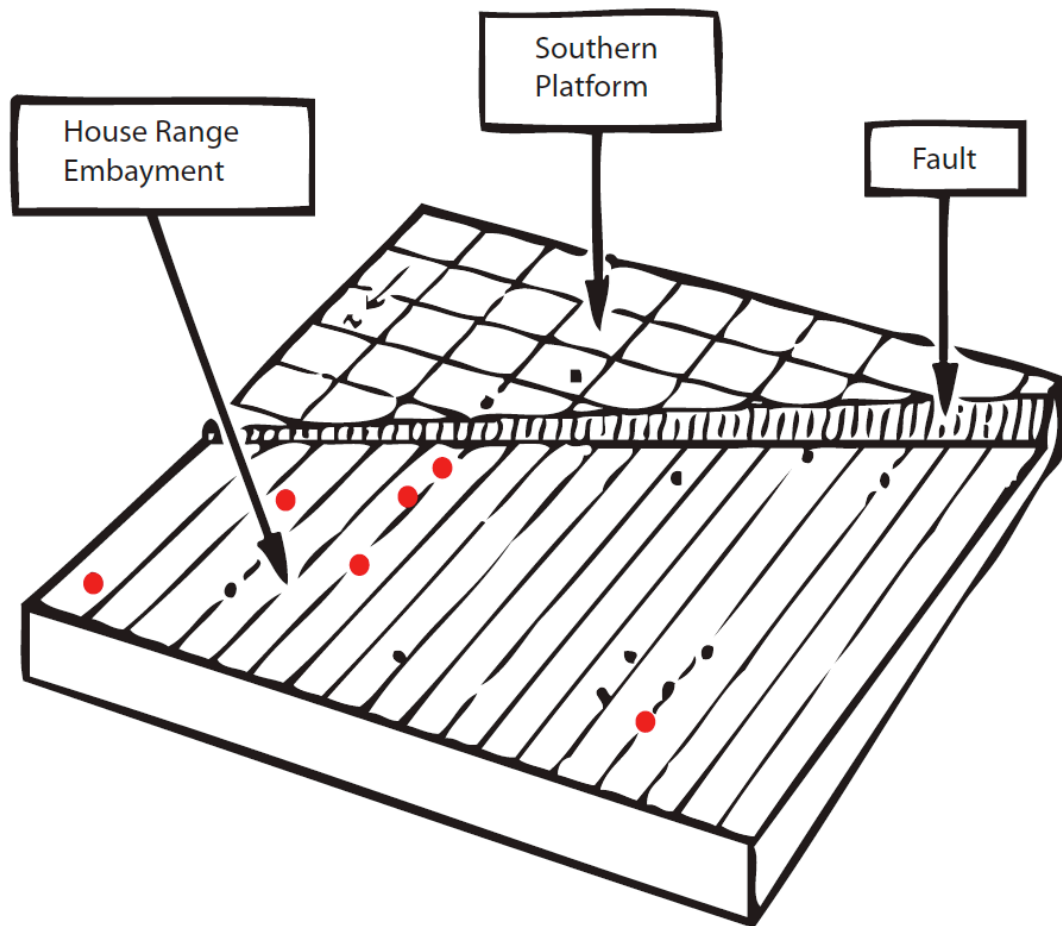


Figure 2.10. Diagram of the House Range embayment, created during the Middle Cambrian due to faulting along its southern margin. Red dots indicate locations where outcrops of Wheeler shale are found. Modified from Rees (1986).

sedimentation consisted of continually shifting carbonate and siliciclastic detrital belts; the House Range of western Utah was represented by a shallow water carbonate shelf (Elrick and Snider 2002). The development of the House Range embayment created an abrupt change in depositional conditions: immediately west of this shallow carbonate shelf was a sharp drop-off into a deep water trough (Fig. 2.10) (the House Range embayment trough; Rees 1986), and opposite this trough was a shallow subtidal carbonate ramp that sloped gently eastward (Fig. 2.10) (the Northern Platform; Rees 1986, Elrick and Snider 2002). The Wheeler Shale is found in both the trough and Northern platform: trough-deposited black shales that are sparsely fossiliferous, preserving mostly agnostic trilobites, and deep ramp platform-deposited carbonaceous shales that preserve a greater diversity of fossils including the BST fauna (Rees 1986; Brett et al. 2009). Robison (1991) identifies two distinct faunas from the Wheeler Shale, the “shallow” and “deep” Wheeler faunas, to distinguish between trough- and platform-deposited material.

Schlottke (2008) performed an ichnofabric analysis of the Wheeler Shale and concluded that Proterozoic-style substrates were the dominant substrate type due to the extremely low levels of bioturbation present. Previous reconstruction of paleoredox conditions in the Wheeler Shale utilizes ichnofacies models (Ekdale and Mason 1988) to establish dissolved oxygen concentrations in the water column. The Wheeler Shale is generally considered to represent dysoxic to anoxic conditions (Rees 1986; Elrick and Snider 2002; Gaines et al. 2003; Brett et al. 2009; Gaines et al. 2012), deposited adjacent to more oxygen-rich waters that supported a benthic fauna (Gaines et al. 2003, 2012). A

previous geochemical analysis of the Wheeler Shale indicated shifting redox conditions from oxic to anoxic in BST-fauna-bearing layers that may have allowed *in situ* preservation of benthic communities (Handle and Powell 2010).

2.3.3 The Maotianshan Shale: The Maotianshan Shale is the middle member of the lower Cambrian Yuanshan Formation of southwestern China (Fig. 2.11) (Chen and Zhou, 1997) which overlies the Shinyantuo Formation, a ~50m thick shallowing upward sequence of siliciclastics. The base of the Shiyantuo Formation likely records a rapid deepening event (Hagadorn, 2002), represented by 10m of dysaerobic black shales (Dornbos et al. 2005); followed by a shallowing event represented by interbedded layers of siltstone and sandstone in the uppermost 40m (Dornbos et al. 2005). Overall the Shiyantuo Formation likely represents a slightly deeper depositional setting than the Yuanshan Formation (Dornbos et al., 2005).

The Yuanshan Formation is the oldest Cambrian stratigraphic unit in the region containing trilobites (Dornbos et al., 2005). It is a 150 km thick sequence of shallowing upward siliciclastics that likely represents deposition in a shallow, tidally influenced marine shelf setting (Chen and Zhou, 1997; Babcock et al., 2001). It is composed of three members: the lower Black Shale Member (20m thick), the middle fossiliferous Maotianshan Shale Member (60m), and the upper Siltstone Member (60m) (Dornbos et al., 2005). The Maotianshan Shale Member features many storm-generated features such as graded bedding, ripple marks, tool marks, and flute casts (Hagadorn, 2002).

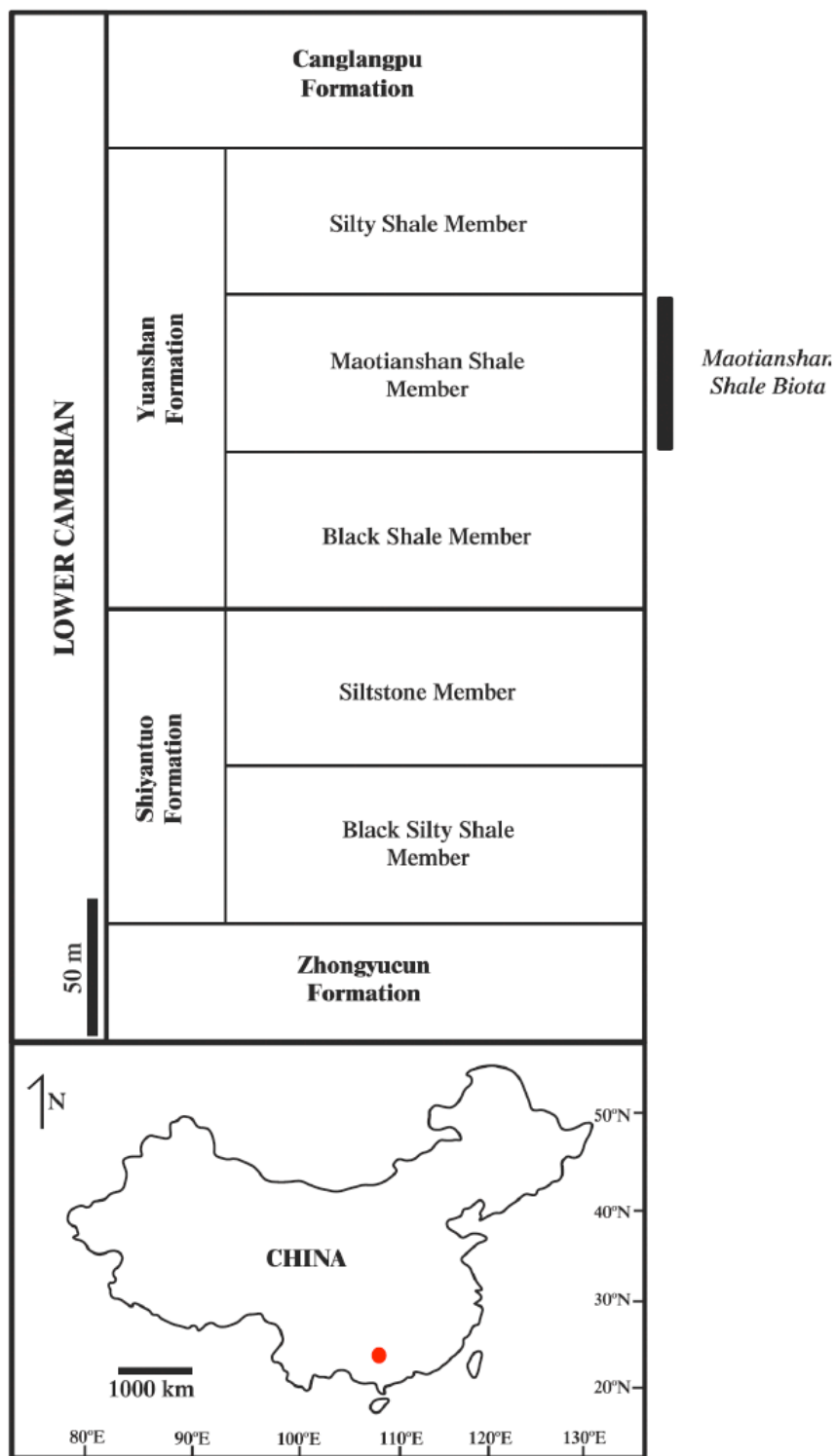


Figure 2.11. Map of China showing location of Maotianshan shale (red dot). Stratigraphic column indicates position of Maotianshan Shale biota within the Lower Cambrian geologic succession in southwest China. Modified from Dornbos et al. (2005).

Fossils in the Maotianshan Shale are generally preserved in beds composed of very thin (1-3mm thick) gray-green to yellow mud layers sharply overlain by a thin layer of clay (Babcock et al. 2001; Hagadorn, 2002). Organisms were likely transported only a minimal distance before final burial; this is supported by observations made on infaunal organisms found still in their burrows (Chen and Zhou 1997) and the preservation of specimens of the cancelloriid *Allonnia junyuani* preserved *in situ* (Kloss et al. 2009). Organisms were likely rapidly buried, as the soft tissues preserved in the Maotianshan generally decay very quickly following an organism's death (Hagadorn, 2002).

Based upon previous paleoecological studies (Dornbos et al. 2005; Kloss et al. 2009), the water column overlying the Maotianshan Shale must have been sufficiently oxygenated to support a diverse benthic marine community. Babcock (2001) hypothesized that exceptional fossil preservation in the Maotianshan resulted from fluctuations in salinity levels inhibiting scavenging and decay of buried organisms.

2.4 Methodology

Samples for this study were collected over several field seasons during 2006, 2008, 2009, and 2010. 1.5m of strata of the Wheeler Shale were collected from the Wheeler Amphitheatre locality in Utah in 2008 and 2009. This material was collected from seven fossiliferous outcrops where numerous taxa were observed, including articulated gogiid echinoderms, articulated cancelloriids, soft-bodied algae *Yukennesia* and *Marpolia*, and several genera of trilobites. Approximately 2.9m of strata of the

Spence Shale was collected from multiple localities in Idaho and Utah—Miner’s Hollow, Oneida Narrows, and High Creek—during 2010. For Miner’s Hollow care was taken to sample localities corresponding to the parasequences of Liddell et al. (1997) in order to compare the results of this study with previous paleoenvironmental interpretations.

2.3m of Maotianshan Shale core sample were collected as part of a Master’s Thesis project in 2006; the core was drilled through the fossiliferous Chengjiang Fauna member of the Maotianshan Shale. Where possible material was chosen that exhibited minimal weathering. Strata was sampled continuously upsection; however, weathering prevented sampling any complete section of either shale; thus the strata will be presented as “composite” sections.

Immediately after excavation samples were wrapped in a protective layer of duct tape to prevent destruction during transport and later lab work. Once at the lab samples were sectioned perpendicular to bedding using a sedimentary rock saw. Part of the sample was retained for use for geochemical analysis, while the rest was utilized for ichnofabric analysis using the ii-method of Droser and Bottjer (1986). Ichnofabrics were analyzed visually on a millimeter-by-millimeter basis and scored on a scale from 1 to 5, 1 indicating complete lack of bioturbation (suggestive Proterozoic-style substrates), and 5 being total homogenization by bioturbation (suggestive Phanerozoic-style substrates). In some cases where the slab face was difficult to observe, an oil immersion technique describe by Savrda et al. (1985) was utilized to enhance visibility.

2.5 Results

Ichnofabric index analysis of the Spence, Wheeler, and Maotianshan Shales are shown in Figs. 2.12-2.15. For complete results of the ii-analysis at the mm-scale, refer to Appendix I. All three shales predominantly exhibit extremely low levels of bioturbation, with 96.9% of the Maotianshan, 92.3% of the Wheeler (1370mm, n=1485mm) and 92.3% of the Spence (2646mm, n=2883mm) scoring 1 with the ii- method (Fig. 16a-c). A fraction of the shale scored 2 (2.7%, 4.8% and 5.5%, respectively) (Fig. 16e) and 3 (0.4%, 2.90% and 2.0%, respectively) on the ii-scale. 0.69% of Spence Shale (Fig. 16d) (located entirely within a single sample of the High Creek locality) scored ii4, but was not recorded in the Maotianshan or Wheeler shales; scores of ii5 were not observed or recorded in the shales over the entire length of the composite sections. As a score of 5 is generally accepted as the threshold for mixed layer development (Dornbos and Bottjer 2000, Dornbos et al. 2005, English and Babcock 2010), the signature of Phanerozoic-style substrates, it is unlikely that Phanerozoic-style substrates were a significant paleoenvironmental factor in the Spence, Wheeler, or Maotianshan Shales.

An attempt was made to observe and record microbially mediated sedimentary structures in the shales (i.e. wrinkle structures, tepee structures, wavy-crinkly laminae, roll-up structures, etc.; see Schieber 1999 for additional information) during ii-analysis. Some individual laminations suggest wavy-crinkly behavior (Fig. 2.17). Evidence of cohesive behavior also exists in several layers in association with what are interpreted

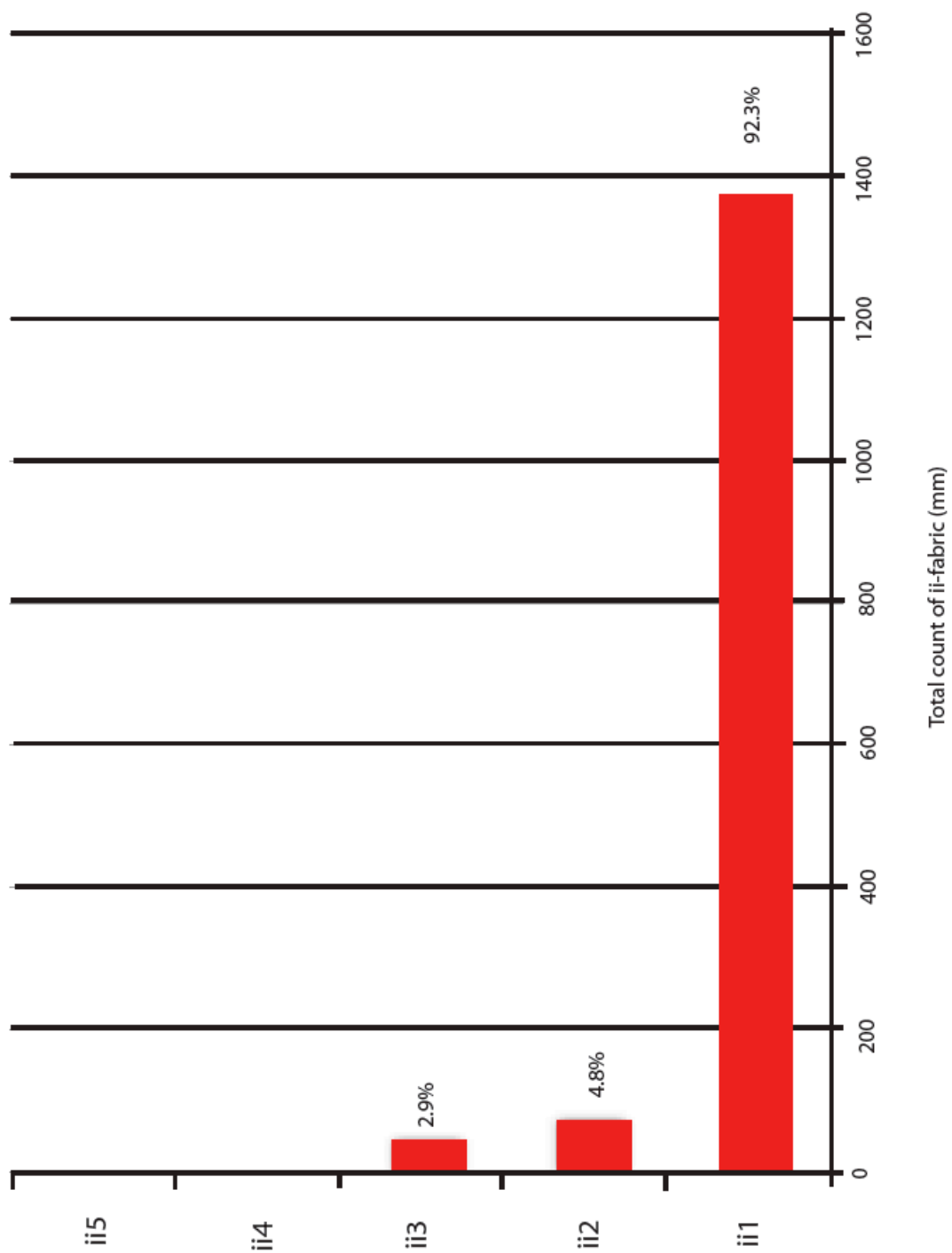


Figure 2.12. Ichnofabric indices analysis for the Wheeler Shale, Wheeler Amphitheatre, Utah. N = 1485.

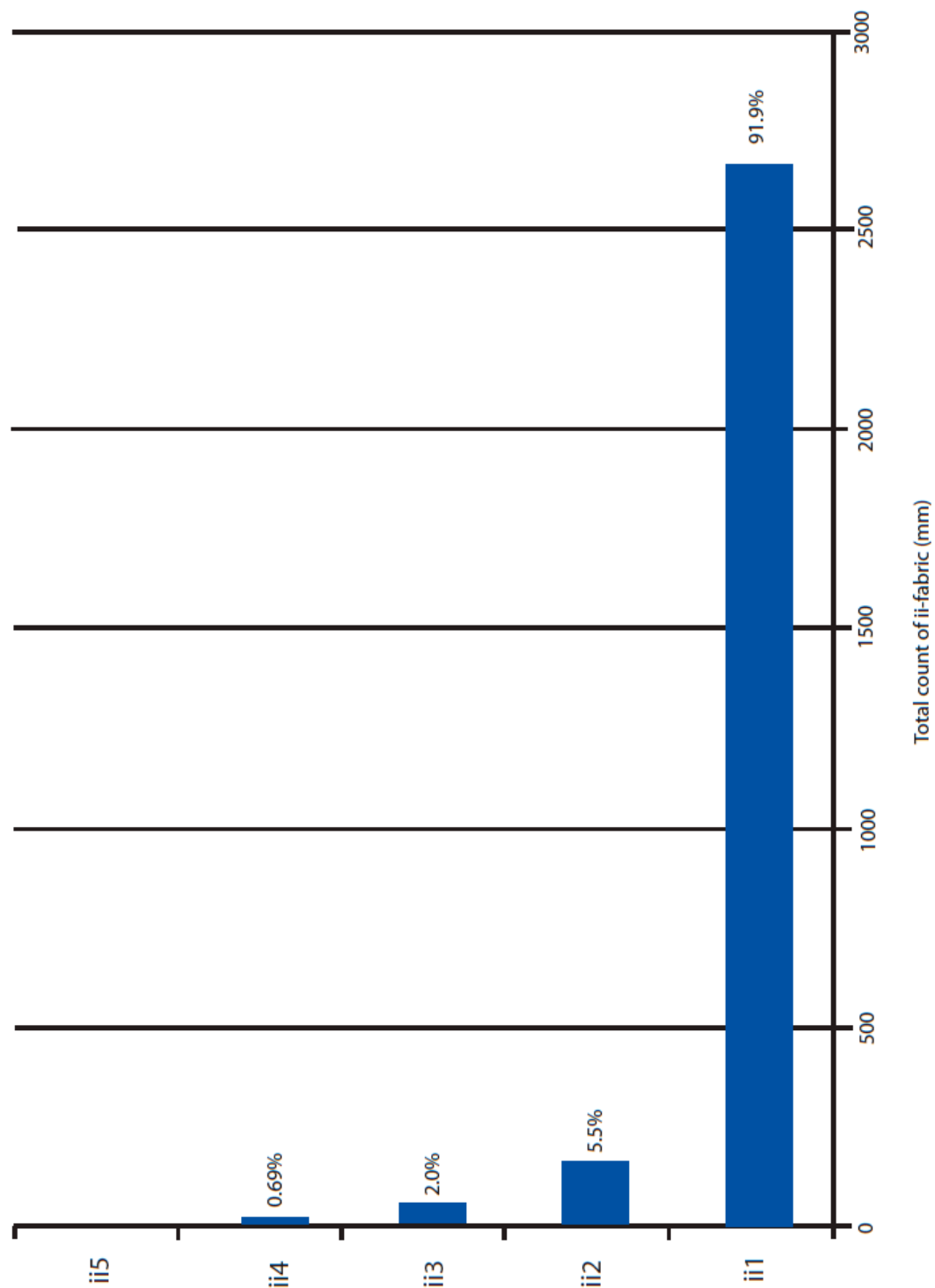


Figure 2.13. Ichnofabric indices analysis for the Spence shale, composite of samples collected at Miner's Hollow, Spence Gulch, Oneida Narrows, and High Creek. N= 2845.

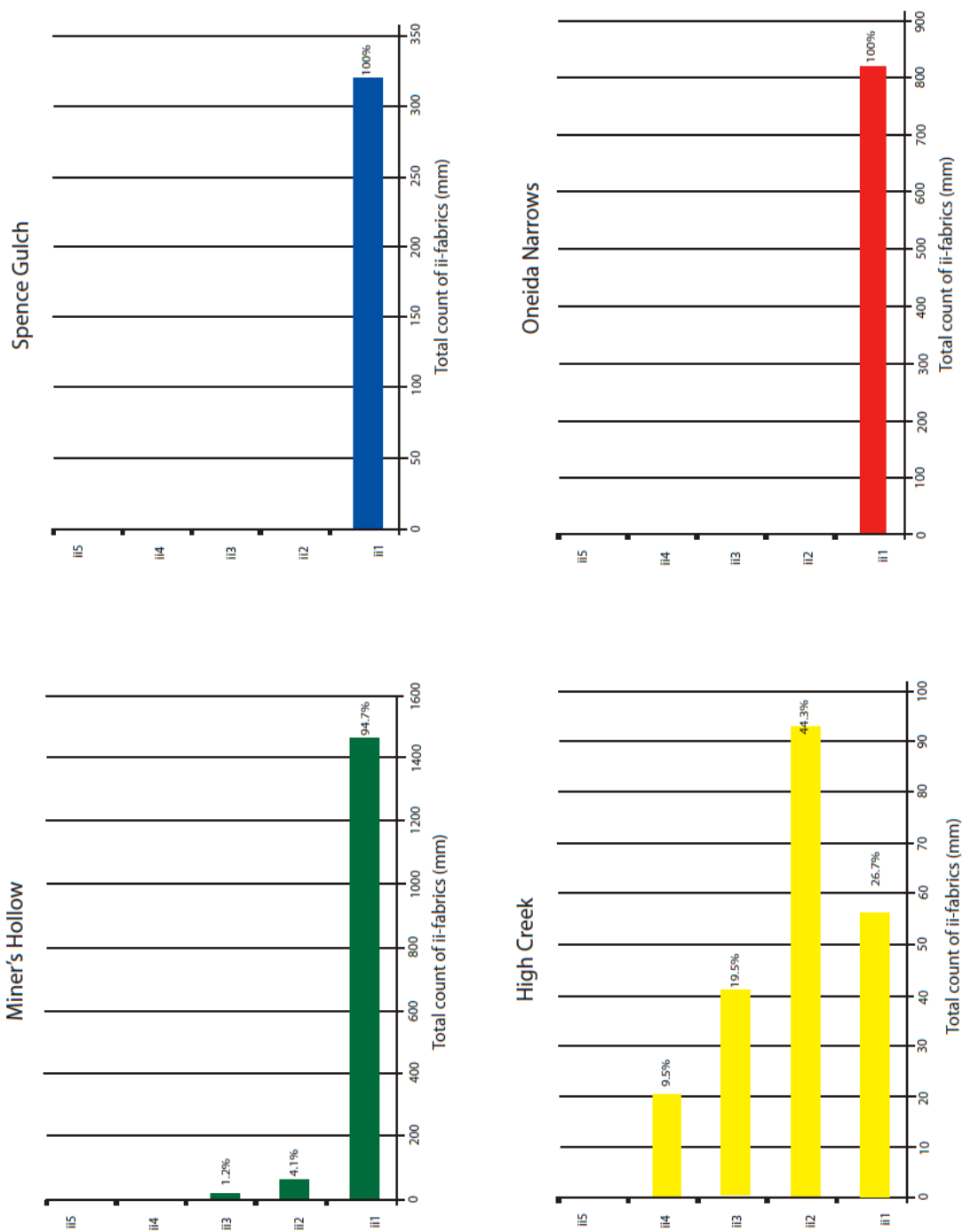


Figure 2.14. Ichnofabric indices analyses of Spence shale by locality. Total counts (n) for each locality: Miner's Hollow = 1546; Spence Gulch = 320; High Creek = 211; and Oneida Narrows = 821.

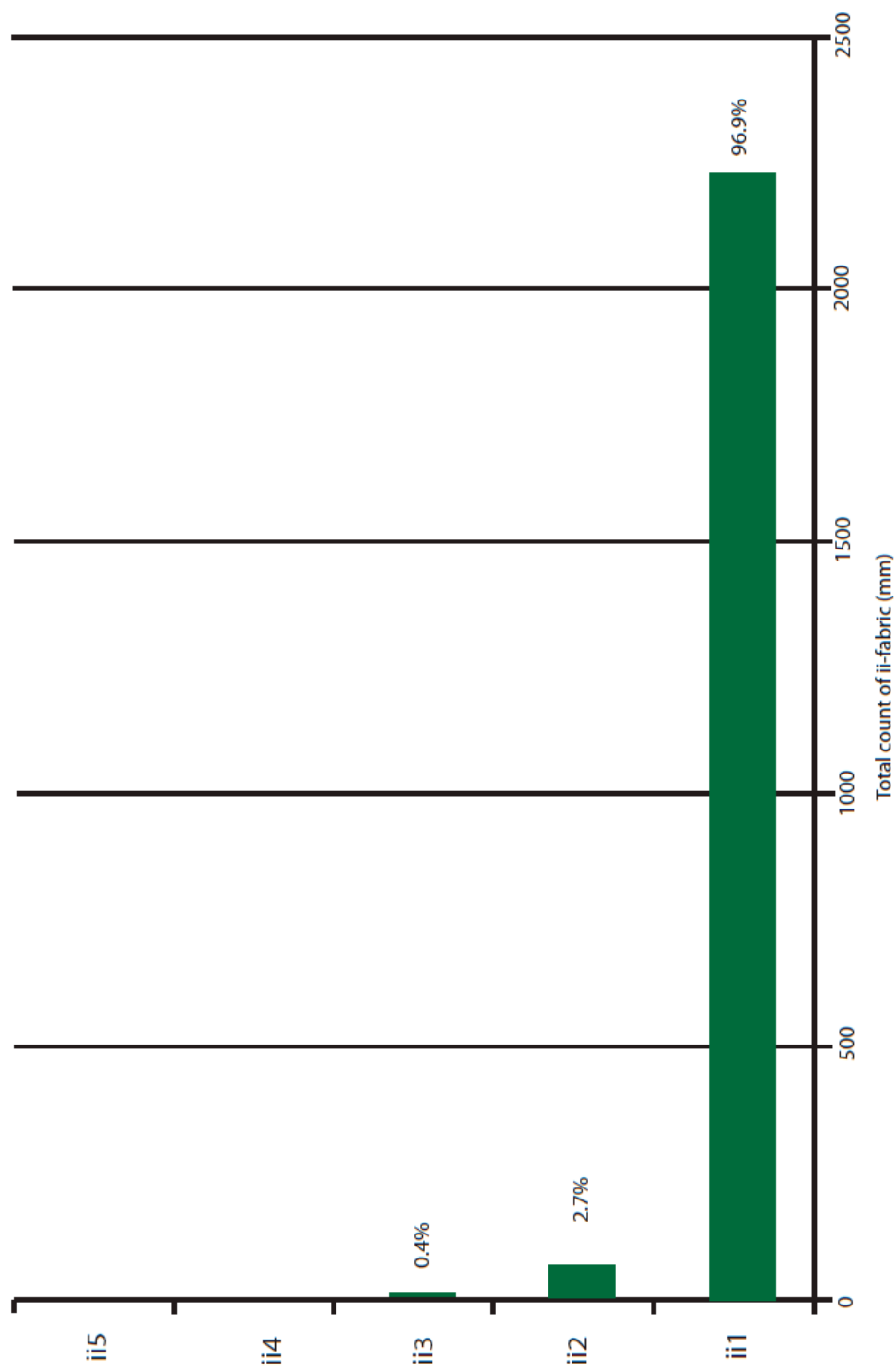


Figure 2.15. Ichnofabric indices analysis for the Maotianshan shale, Yunnan Province, China. Data compiled from Kloss et al. (2009). N= 2301.

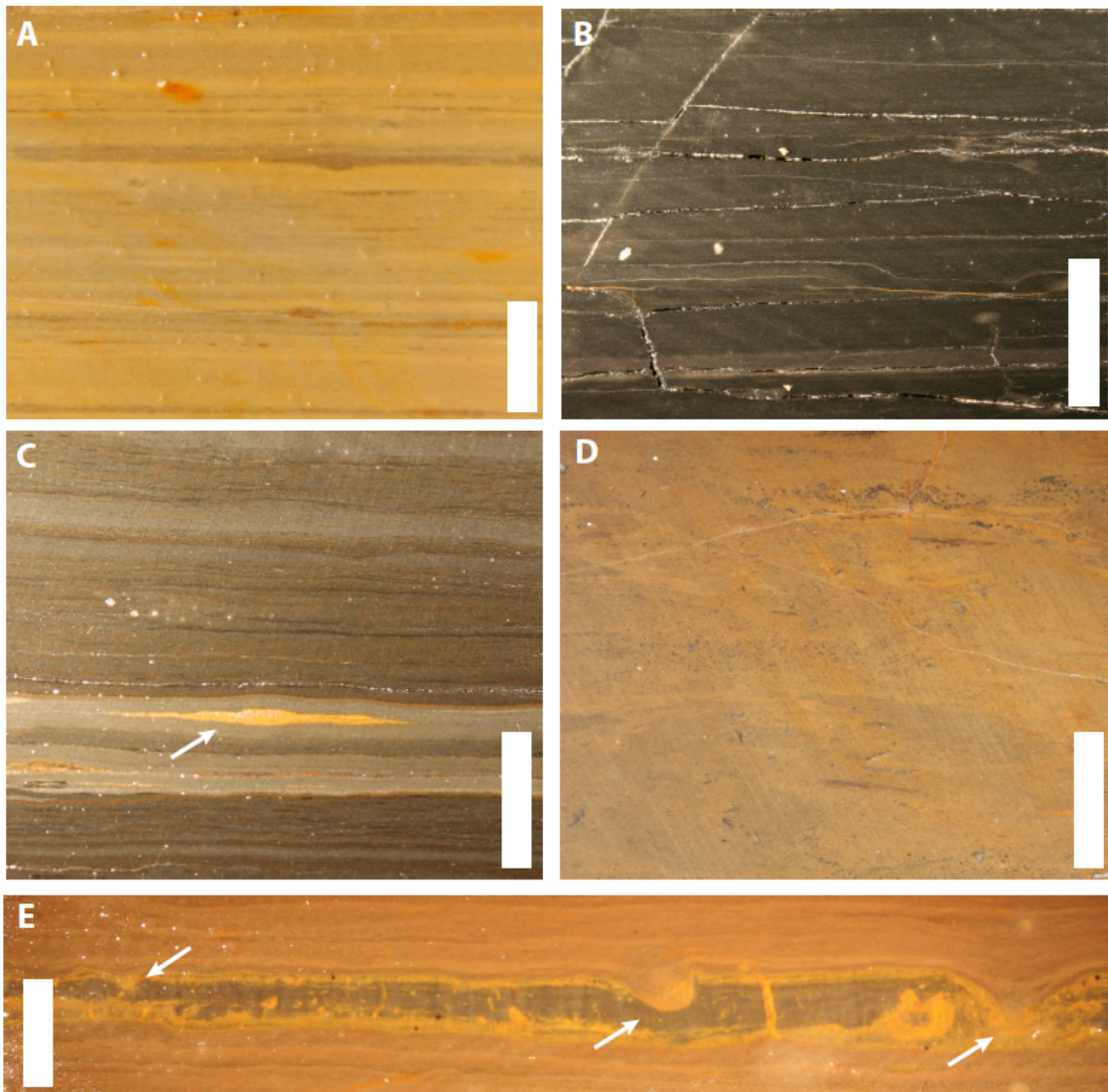


Figure 2.16. Examples of ii-fabrics observed in the Wheeler and Spence shales. A: ii1 fabric, W5D, Wheeler shale. B: ii1 fabric, SG2A, Spence shale. C: ii1 fabric, ON2B, Spence shale. Concentrations of pyrite are evident (arrow). D: ii4 fabric, mottled and bioturbated sediments found at the High Creek locality, Spence shale. This maximum amount of bioturbation recorded was restricted to a single sample (HC2A, shown here). E: ii2-ii3 fabric, W5H, Wheeler shale. Note several distinct burrows (arrows) crosscutting a small bedding layer, with ii1 fabrics surrounding the burrowed layer. Bioturbation generally is restricted to small mm-scale intervals surrounded by extensive ii1 fabrics. Scale bars = 1cm.

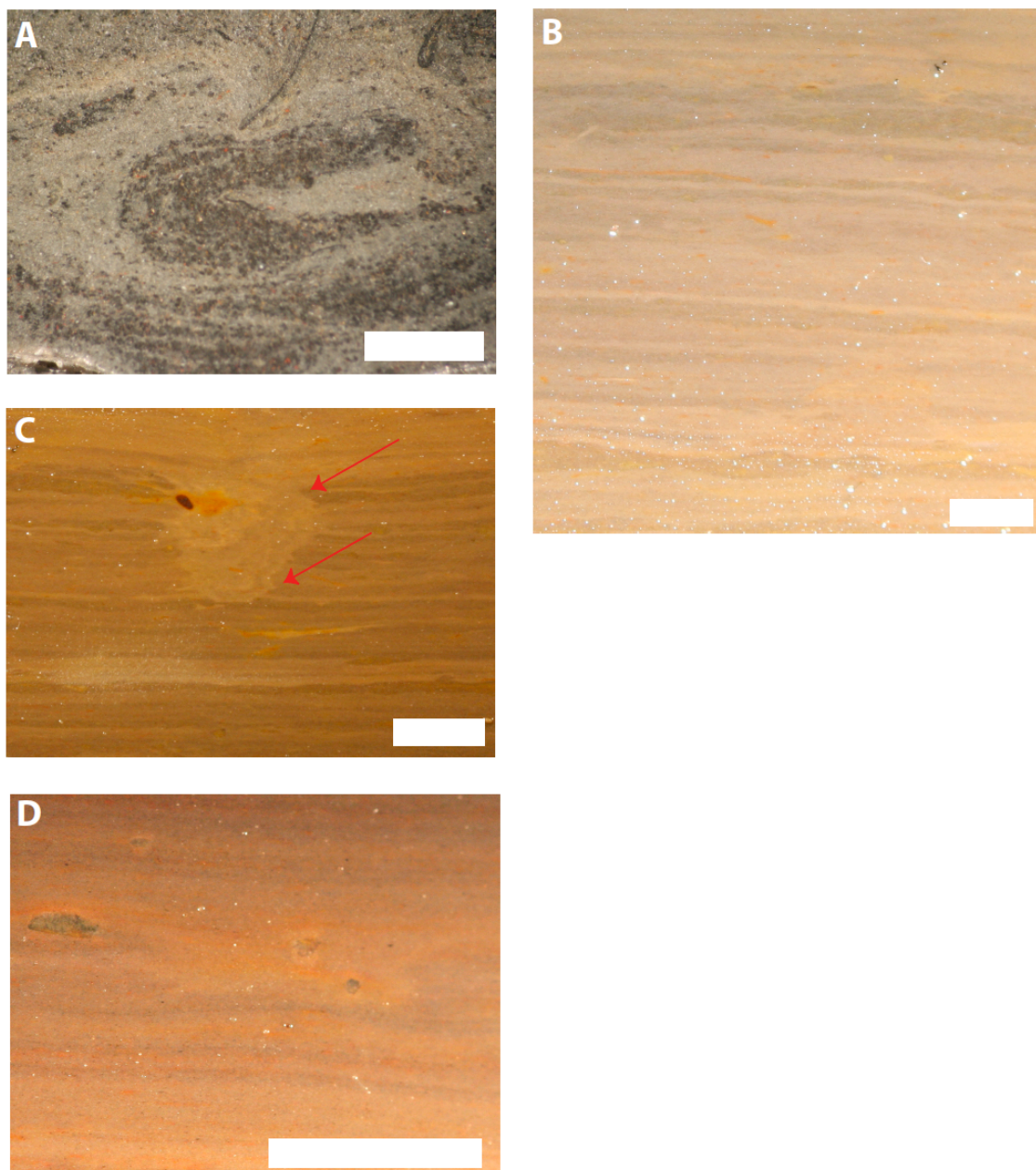


Figure 2.17. Sedimentary features suggestive of microbial mediation observed in the Wheeler and Spence shales. A: Folded/roll-up structure in LMH3B; B: wavy- crinkly laminae exhibiting irregular width (ii1) in W5H. C: Burrow (?) or scour structure crosscutting through multiple laminations (ii1); note the irregular boundary and feathering of laminae (arrows) in contact with burrow, suggesting cohesive behavior of the substrate. D: Burrow (?) or scouring structure crosscutting laminae in the same manner as C; irregular boundary and feathering is apparent. Scale bars = 5mm. Reflectivity apparent in some images are the result of oil immersion technique to highlight sedimentary structure.

as either burrowing structures or possibly some form of scour mark (Fig. 2.17c, d). This structure shares a sharp contact with the surrounding substrate, and laminations that are crosscut by the structure display frayed, angular edges consistent with cohesive behavior. In addition, roll-up structures are also present but rare (Fig. 2.17a). The overall results of this analysis are similar to other fine-grained siliciclastic Cambrian units where Proterozoic-style substrates are suspected: the Maotianshan Shale, the Chisholm Shale, and the lower member of the Poleta Formation (Dornbos and Bottjer 2000; Dornbos et al. 2005; Domke and Dornbos 2010).

2.6 Discussion

The transitional nature of marine substrates in association with the agronomic revolution allows for the lack of bioturbation observed in the Spence, Wheeler, and Maotianshan Shales to be interpreted in one of two ways: 1) Proterozoic-style substrate conditions dominated the depositional environment of all three shales, precluding the presence of bioturbation (i.e. substrate control); or 2) anoxia dominated the depositional environment of all three shales, inhibiting bioturbation (i.e. redox control). Measurements of ichnofacies in the Spence, Wheeler, and Maotianshan Shales conducted by other workers (Gaines and Droser 2004, Garson et al. 2008, Brett et al. 2009, Garson et al. 2012), suggest that the absence of bioturbation is due to a lack of dissolved oxygen concentrations (DOC) in the overlying marine bottom waters leading to conditions of anoxia or euxinia (Gaines and Droser 2004; Brett et al. 2009). The

general context of most ichnofacies interpretations is decidedly Phanerozoic-centric, having been designed from observations of typical Phanerozoic-style substrates and from modern marine settings (i.e., Savrda and Bottjer 1987; Ekdale 1988). In normal marine Phanerozoic benthic environments DOC will play a significant role in controlling the activity of benthic and infaunal metazoans, and common ichnofacies assemblages (i.e. *Cruziana*, *Skolithos*, *Trypanites*, *Zoophycos*, etc.) have demonstrable effectiveness as proxies for paleobathymetry and paleoredox conditions in normal marine settings during much of the Phanerozoic (e.g. Frey and Pemberton 1990; Miller 1991; Zhao et al. 1997; Nesbitt and Campbell 2006; Nagendra et al. 2010). The majority of the Cambrian period, however, is not comparable to the environmental and ecological history of the rest of the Phanerozoic; the Cambrian radiation and agronomic and Cambrian substrate revolutions are events unique to this period, leading to substrate conditions that are demonstrably nonactualistic in many cases (Seilacher and Pflüger 1994; Bottjer et al. 2000; Dornbos and Bottjer 2001; Droser et al. 2002; Parsley and Prokop 2004; Dornbos et al. 2005; Domke and Dornbos 2010; English and Babcock 2010). Therefore one should expect to find many Cambrian marine settings where bioturbation is minimal or absent and Phanerozoic-style substrates are not observed, but this does not necessarily indicate the presence of anoxia.

Ichnofabric index analysis of the Spence, Wheeler, and Maotianshan Shale substrates suggests the presence of Proterozoic-style substrates. Bioturbation was noted at several locations within both sections, but in all cases the bioturbation was extremely shallow, penetrating no more than a few millimeters through the substrate

and in some cases failing to completely burrow through individual laminations (Fig. 2.17c), similar to the simple shallow burrows found in Proterozoic-age sediments associated with the Ediacaran fauna (Narbonne 1998, Jensen et al. 2005; Seilacher et al. 2005; Buatois and Mangano 2011). Evidence for the cohesive behavior of sediment suggests that microbial mats may have influenced at least in part the development of substrates in the shales, though such evidence is limited. The dearth of microbial mat evidence does not invalidate the putative existence of Proterozoic-style substrates; numerous other Proterozoic-style substrates typically lack microbial mat structures (Dornbos and Bottjer 2000; Dornbos et al. 2005; Kloss et al. 2009; Domke and Dornbos 2010), and microbial mat development is not a prerequisite for Proterozoic-style substrates, although it likely aids in maintaining substrate conditions by inhibiting the colonization of the substrate by burrowing organisms (Bailey et al. 2006). Fine-grained Cambrian siliciclastics were cohesive enough on their own to account for the presence of Proterozoic-style substrates, due in part to the embryonic nature of Cambrian sediments prior to the period of extensive bioturbation (Droser et al. 2002). The lack of convincing evidence for the colonization of the environment by microbial mats means that the interpretation of Proterozoic-style substrate conditions is not definitive, and that anoxia may have still played a role in controlling bioturbation in the Spence, Wheeler, and Maotianshan Shales.

The Spence, Wheeler, and Maotianshan Shales preserve soft-bodied BST-type faunas with numerous benthic taxa including echinoderms, sponges, and some enigmatic fossils (Robison 1991). Several of these taxa have been directly observed

exhibiting adaptive strategies consistent with Proterozoic-style substrates, including the eocrinoid *Gogia spiralis* and two species of chancelloriid, *Chancelloria eros* and *Allonnia sp.* (Schlottke 2008; Kloss et al. 2009), and a literature review of remaining taxa also reveals morphologies that suggest attachment under the influence of Proterozoic-style substrates (Robison 1965; Rigby 1983; Dornbos et al. 2005; Rigby et al. 2010) (see following chapter for a comprehensive discussion of the paleoecological analysis for these localities). At the same time there are numerous organisms that were likely adapted to Phanerozoic-style substrates by the middle Cambrian (next chapter), and thus typical Phanerozoic-style environments were also present. Paleocology thus offers a similar interpretation to these environments as the one provided by ichnofabrics: both Proterozoic- and Phanerozoic-style substrates may have been present in Cambrian marine settings.

Varying interpretations of sedimentological and paleoecological data make it difficult to render a definitive interpretation of substrate conditions in the Spence, Wheeler, and Maotianshan Shales. Understanding the timing and distribution of the agronomic revolution, and how long transitional substrate conditions persisted into the Cambrian, would help resolve issues of substrate interpretation for these marine shales. Proterozoic-style adaptive strategies are present among benthic metazoans in many middle Cambrian shales, and Cambrian paleoenvironmental interpretations should take into consideration the effect of the agronomic revolution at least until this period of time. In such cases other analytical approaches should be considered to resolve the above challenges; here it is proposed (and demonstrated in subsequent chapters) that

geochemical analysis of paleoredox conditions, in combination with sedimentological and paleoecological analysis, can place the Spence and Wheeler Shale substrates into a proper paleoenvironmental context.

2.7 Conclusions

The ichnological analysis of the Spence, Wheeler, and Maotianshan Shale substrates demonstrates that:

- 1) Shales demonstrate extremely low levels of bioturbation (~ii1) and sedimentary fabrics consistent with Proterozoic-style substrates per Droser and Bottjer (1986);
- 2) Microbial mats were present but uncommon in the marine environments of the Spence, Wheeler, and Maotianshan Shales, thus the development of Proterozoic-style substrates was controlled both by a lack of bioturbation and the development of microbial mat cover;
- 3) The putative presence of Proterozoic-style substrates is supported by the adaptive morphology of the benthic faunas associated with the Spence, Wheeler, and Maotianshan Shales;
- 4) These ichnological results are consistent with analysis via ichnofacies by other workers, but...
- 5) ...interpretations vary regarding the controlling factor on the lack of bioturbation (i.e. substrate versus redox);

- 6) The utilization of applying ichnofacies models and ichnofabric indices to Cambrian substrates is dependent upon the time-sensitive nature of the agronomic revolution;
- 7) Interpretations of Cambrian paleoenvironments based upon sedimentological and paleoecological data may not be enough, and additional analytical approaches including geochemical analysis may be necessary to properly interpret these geologically unique substrates.

CHAPTER 3: PALEOECOLOGY OF CAMBRIAN SHALE COMMUNITIES

Since stability atop the marine seafloor is essential to the survival of benthic metazoans, analysis of morphological strategies can determine the physical nature of the substrate upon which these organisms were living. A literature review of 16 benthic faunal assemblages from the Cambrian and Ordovician analyzed the morphological strategies exhibited by sixty different benthic genera and placed them into one of two categories: 1) Proterozoic-style adaptive strategy, or 2) Phanerozoic-style adaptive strategy. Based upon the strategies observed, it appears that Proterozoic-style substrate conditions were still present and influential in the development of benthic metazoan ecology at least until the end of the Middle Cambrian, and possibly persisted into the late Cambrian period. Metazoans exhibiting Phanerozoic-style adaptive strategies steadily increased through the Cambrian, reaching total dominance by the late Cambrian period. Most early and middle Cambrian shales preserved benthic genera with a mix of Proterozoic- and Phanerozoic-style adaptive strategies, suggesting substrates reached a transitional state that likely saw the coexistence of both substrate conditions at this time. While this information is useful for broad paleoenvironmental interpretations of Cambrian settings, the *in situ* nature of some benthic assemblages, including the Maotianshan (Chen and Zhou 1997), confirm the presence of Proterozoic-style substrates in these settings derived from ichnofabric analysis and is generally

suggestive that Proterozoic-style substrate conditions still played a vital role in the development of marine settings for much of the Cambrian period.

3.1 Morphological adaptations of benthic metazoans to substrate conditions

Substrate conditions play a role in controlling the behavior and morphological adaptations of benthic metazoans. Most burrowing organisms, for example, are restricted to soft marine substrates or evolve specific adaptations for burrowing into hard substrates (i.e. modification of valve morphology on wood-boring “shipworm” mollusks and coral boring bivalves; Kleemann 1996; Evans 1998). For sessile filter feeding benthic metazoans their relationship to the marine substrate is of greater significance, as most of these organisms are unable to relocate if conditions change unfavorably and initially locating suitable substrate conditions during the mobile larval stage prior to attachment is critical for survival. For the sessile filter feeding metazoan a suitable attachment site should: a) elevate the metazoan to a proper height above the seafloor to effectively feed; and b) provide necessary stability in order to avoid collapsing, toppling, or otherwise being reoriented into an unsuitable position under normal environmental conditions. To a large extent these two qualifications must be met through morphological adaptation of the metazoan, i.e. attachment disks, stalks, arms, etcetera; however the general substrate conditions present in the marine environment will control the adaptive measures of the metazoans.

As Proterozoic- and Phanerozoic-style substrates are remarkably different in physical conditions, one would expect that benthic metazoans would find unique but separate adaptive morphologies for each. Thayer (1975) described four distinct adaptive strategies of modern benthic metazoans from a soft substrate marine setting that is prototypical of Phanerozoic-style substrates. These adaptive strategies include:

- 1) *Hard substrate attachment*. The metazoan attaches directly to a hard substrate such as rock, coral reef, or exposed skeletal material through varying means, e.g. the brachiopod pedicle, barnacles that grow directly on hard surfaces or attach by means of a stalk (Doyle et al. 1997).
- 2) *Root-like holdfast*. Development of root-like cirri or other structures that embed some depth into the substrate and increase drag during attempted uprooting events (Fig. 3.1). Many species of crinoid are well known for this style of adaptation, although some sponges and also algae (“seaweed”) also exhibit root-like holdfast structures (Milligan and Dewreede 2000; Seilacher and Macclintock 2005).
- 3) *Iceberg Strategy*. The metazoan utilizes a long skeletal extension inserted into the substrate. At greater depths the density of the substrate increases sufficiently to stabilize the metazoan at the surface (Fig. 3.2). The crinoid *Isselocrinus* uses a variation of this technique by continually attaching itself to previous sections of broken columnal stalk (Fujiwara et al. 2005).
- 4) *Snowshoe strategy*. The metazoan grows to a very large size or has a very high rate of growth (or both), sufficient enough that it will remain buoyant

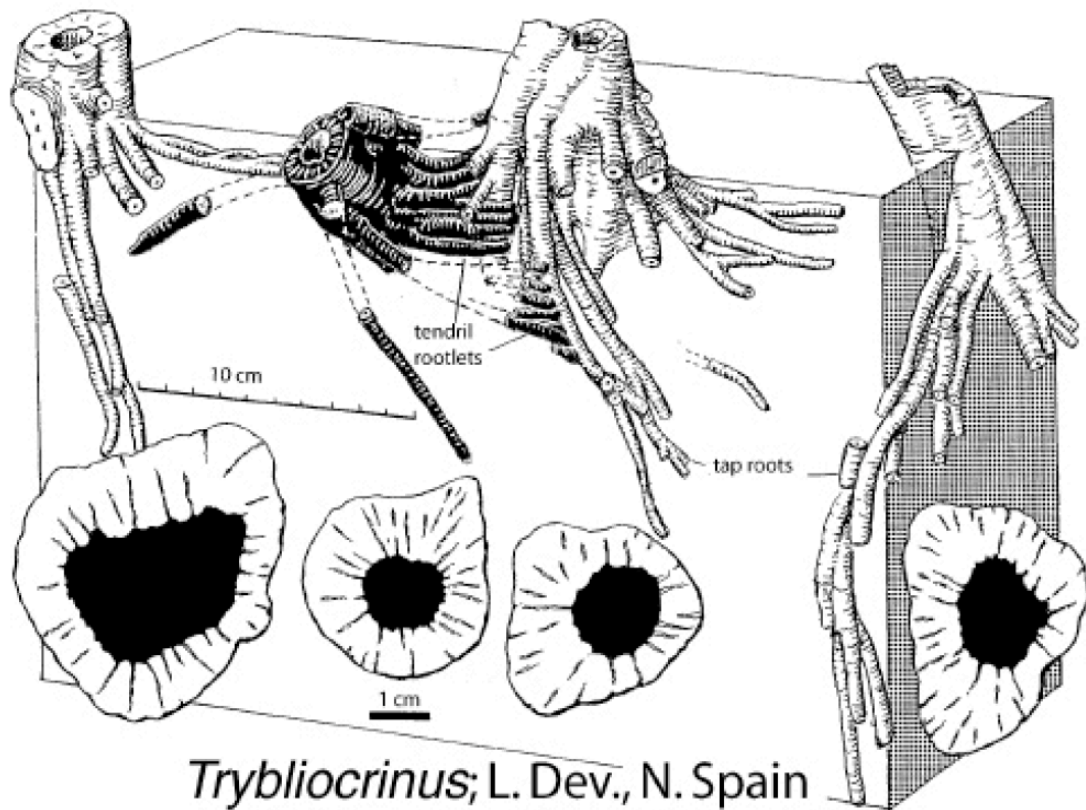


Figure 3.1. Illustration of the root-like holdfasts of crinoid genus *Trybliocrinus* from the early Devonian. Rootlike holdfast structures aid in stabilization of immobile benthic metazoans on soft, soupy Phanerozoic-style substrates. Modified from Seilacher and Macclintock (2005).

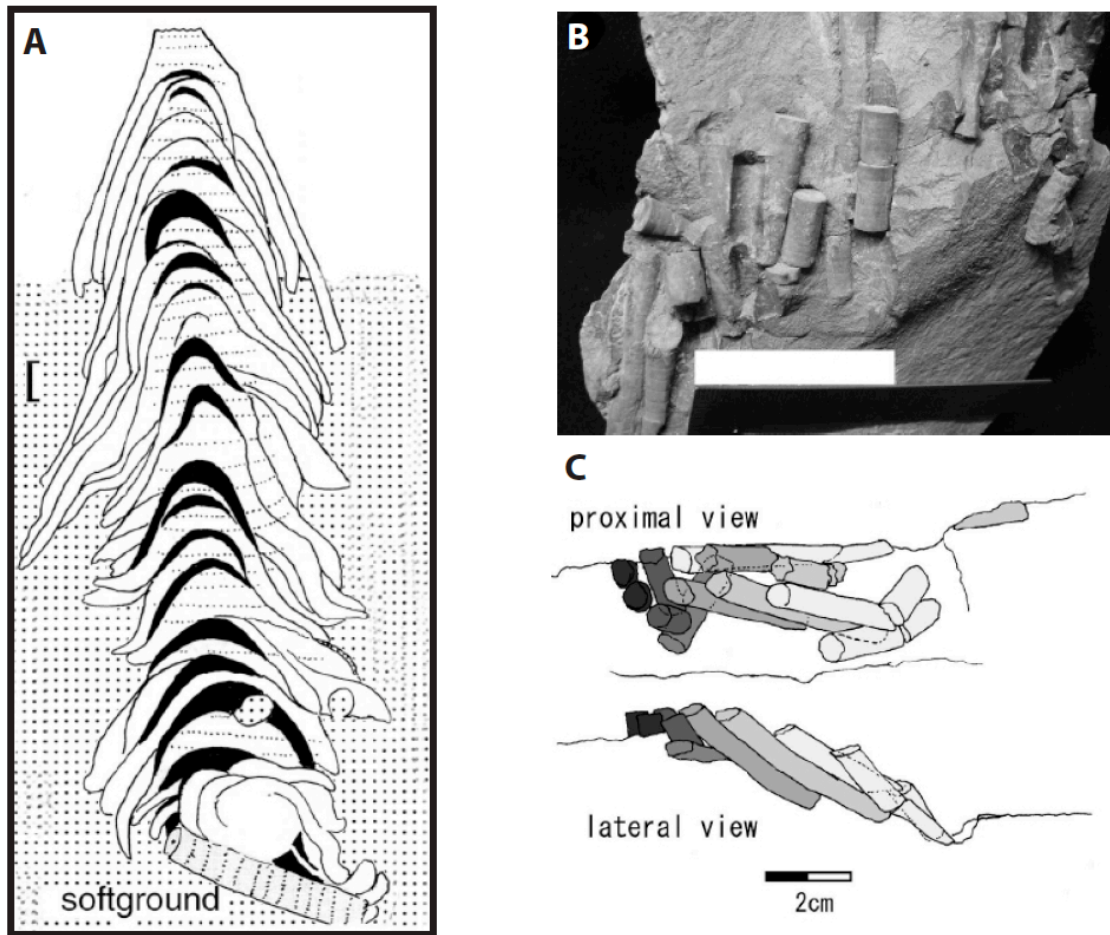


Figure 3.2. Examples of the iceberg strategy among crinoids. A: Stacked cone strategy utilized by genus *Apiocrinites* of the Upper Jurassic, England. The basal anchor in this genus is continually regenerated in response to sedimentation, creating a much larger composite anchoring structure over time. B, C: Relay strategy utilized by genus *Isselicrinus* of the Upper Eocene, Japan. This genus utilized reattachment of basal end to earlier extensions of the stalk, creating large bundles of interconnected material that served to anchor the individual in soft substrates. Scale bar in B = 5cm. A is modified from Seilacher and Macclintock (2005), and B/C are modified from Fujiwara et al. (2005).

atop the substrate and not become smothered by sediment deposition.

Some bivalves are known for using this strategy, growing to immense size (Thayer 1975).

A number of early-middle Cambrian metazoans have long been recognized as having unusual body plans which make them difficult to classify (i.e. 'problematica') (Whittington 1975; Whittington and Briggs 1985; Briggs and Conway Morris 1986; Gould 1989; Ramskold and Hou 1991; Chen et al. 2005) and discussion has focused on the factors leading to the evolution of these unusual morphologies and the circumstances that lead to their disuse among extant phyla. In his treatise *Wonderful Life* (1989), Gould considered the vexing nature of Cambrian fauna and hypothesized that such unusual body plans were evolutionary quirks or "experiments" in the history of life, developed at a time when selective pressures were considering all possible morphological schemes on the way to modern functioning ecosystems. Gould saw all of life during the Cambrian Radiation as a great experiment, and only through random chance did some morphologies persist until the present day while others became labeled as "failed experiments" known only through fossil remains (Gould 1989) (Fig. 3.3).

Once the agronomic revolution was recognized by Seilacher and Pflüger (1994), our conceptions regarding these unusual creatures underwent their own "revolution." Re-examinations of the morphologies of a number of fossil taxa revealed adaptations for survival on Proterozoic-style substrates. These adaptive strategies differ from those

identified by Thayer (1975, 1983) in modern marine substrates, and are described by Dornbos et al. (2005):

- 1) *Sediment Sticker*. The metazoan directly embeds its distal end into the sediment without any obvious means of attachment (i.e. root-like holdfasts, attachment disks, etc.) and not to a depth great enough to be considered an iceberg strategy (Thayer 1975) (Fig. 3.4c). The substrate itself appears to be sufficiently stable to support the weight of the metazoan without the need for additional morphological structures. The cancelloriids (Kloss et al. 2009) and some groups of eocrinoids (Parsley and Prokop 2004; Schlottke 2008) appear to use this strategy.
- 2) *Sediment Attacher*. The metazoan directly secures itself to the substrate using a suction-cup-like suctorial disk (Fig. 3.4a). The substrate would need to be cohesive enough to allow for adhesion to the seafloor through suction. The edrioasteroid *Totiglobus* (Domke and Dornbos 2010) utilized sediment attachment.
- 3) *Sediment Rester*. The metazoan passively rests upon the sediment surface without obvious means of attachment (Fig. 3.4b). Possibly the Proterozoic-style analogue to the snowshoe strategy of Thayer (1975). Several genera of Cambrian sponge (*Choia*, *Crumillosporgia*) were sediment resters (Dornbos et al. 2005).

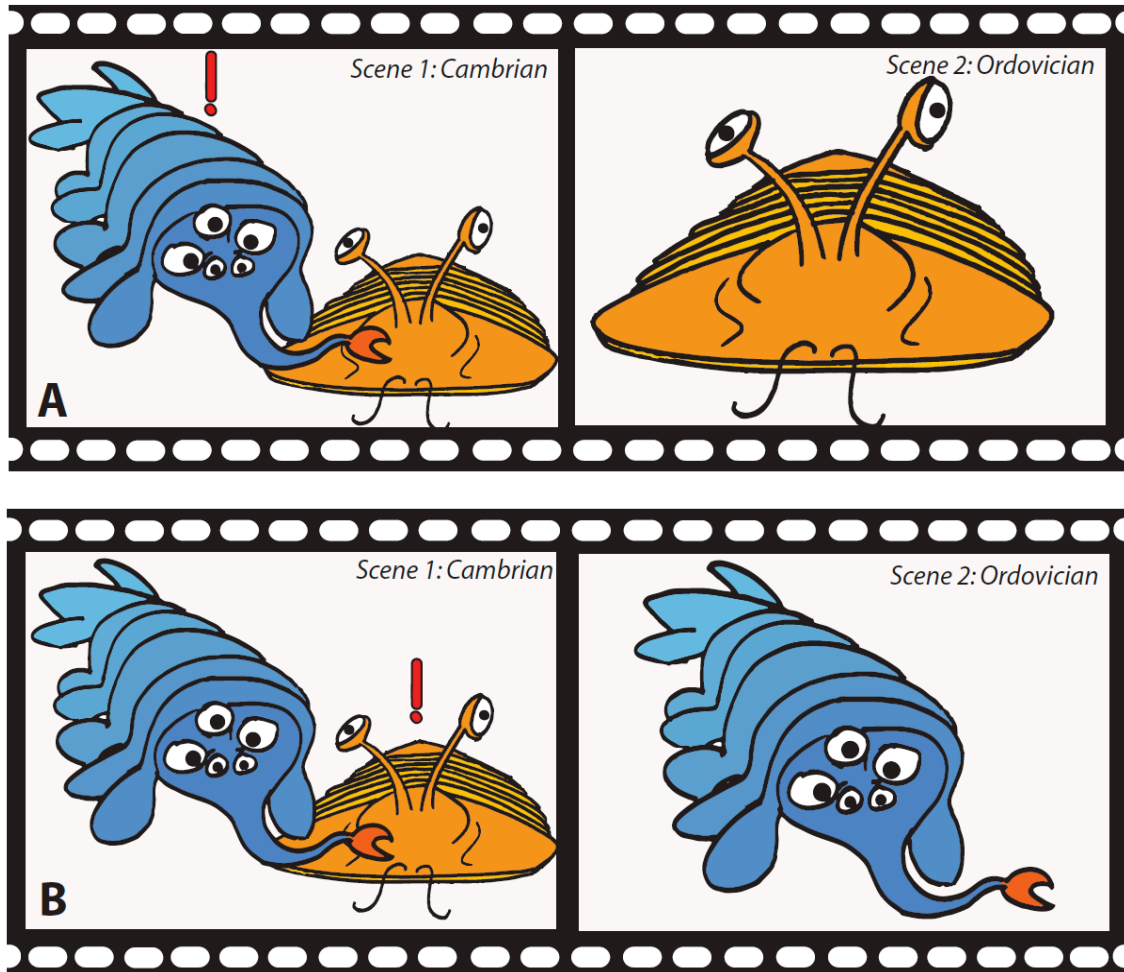


Figure 3.3. As part of his “failed experiments” hypothesis regarding the “unusual” morphologies observed among early Cambrian metazoans, Stephen Jay Gould used the analogy of a movie to describe the history of life. We know the actual outcome of multitude of geologic events that are represented in the fossil record: *Opabinia* is extinct by the end of the Cambrian, while trilobites persist through the Paleozoic (A). If the countless number of environmental and geological events involved in the development of life were to have different outcomes, Gould argued, then perhaps some of the “failed” metazoan morphologies would have instead proven successful; *Opabinia* may have been a survivor out of the Cambrian, and trilobites instead went extinct (B).

In addition to sessile benthic metazoans, some mobile benthic metazoans are notable for exhibiting behaviors or morphologies that are only logical in association with Proterozoic-style substrates. Mono- and polyplacophoran mollusks, for example, are *mat grazers* that rely upon microbial communities for sustenance; their presence in shallow subtidal substrates during the Cambrian is perplexing unless a microbial mat food source was also present (Bottjer et al. 2000). The unusual coeloscleritophoran *Wiwaxia* is another likely mat grazer, based upon traditional ecological interpretations and its presence in fine-grained muddy siliciclastics (Conway Morris 1985; Dornbos et al. 2005). A second adaptive strategy observed in some mobile benthic metazoans is *mat walking*, where the legs/ambulatory structures of the metazoan are adapted for locomotion across relative firm substrates, making walking in softer, bioturbated sediments unnecessarily difficult. Lobopodians such as *Hallucigenia*, with its short unjointed legs, are a typical example of this mat walking lifestyle.

It should be noted that the Proterozoic-style adaptive strategies are dependent upon the existence of firm, cohesive substrates in order to be successfully utilized, whereas the Phanerozoic-style adaptations may conceivably be utilized on Proterozoic-style substrates as well. Utilization of Phanerozoic-style adaptive strategies likely did not evolve until after the initiation of intense burrowing during the agronomic revolution, however, as they have additional ecological costs without any significantly added benefit. The single exception may be hard substrate attachment, as some exoskeletal material (e.g. the Small Shelly Fauna) predates the Cambrian radiation and may have provided some evolutionary advantages to benthic metazoans facing competition for

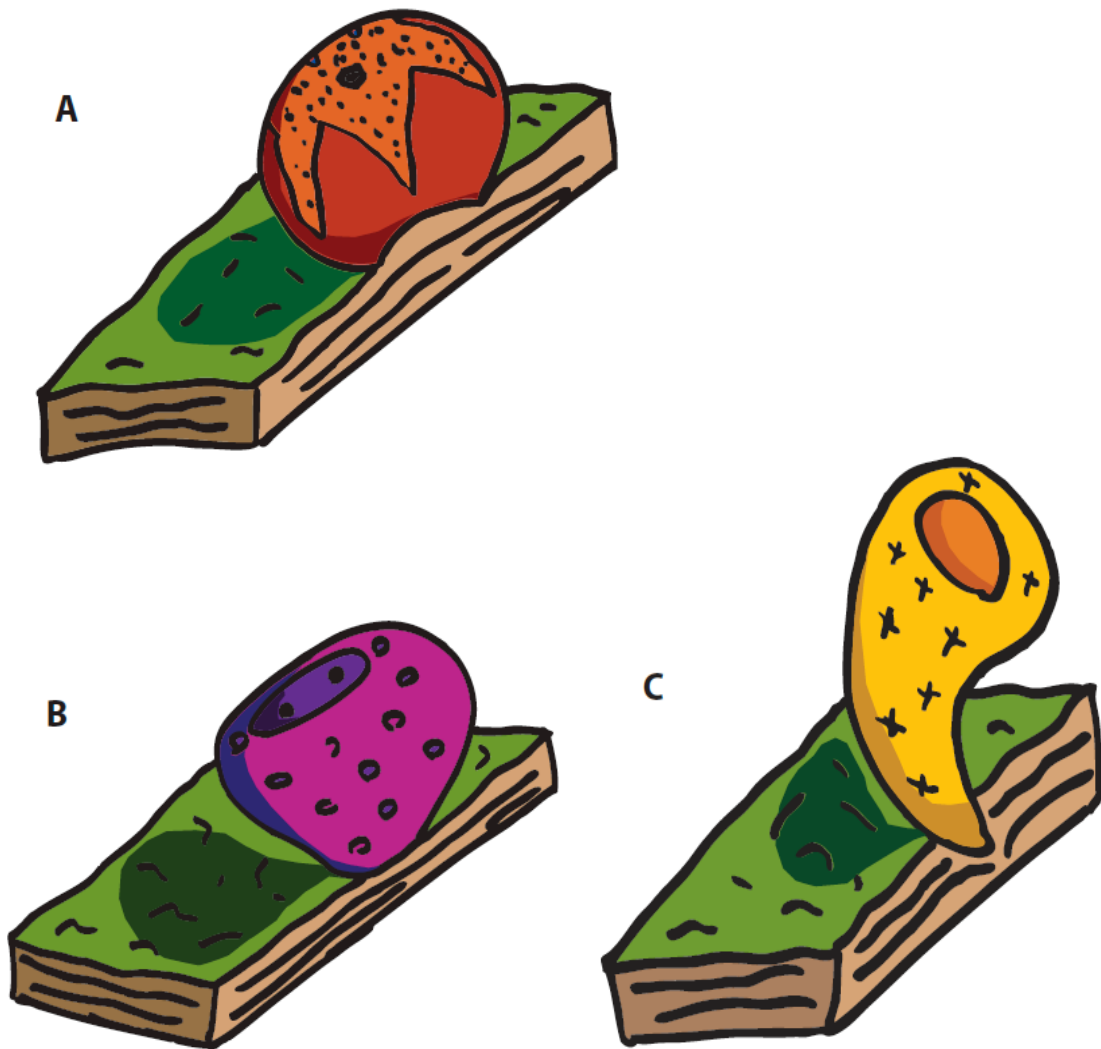


Figure 3.4. The three methods of attachment utilized by immobile benthic metazoans on Proterozoic-style substrates. A: sediment attaching, where the organism directly attaches to the substrate by either using an bio-adhesive or a suctorial disk (i.e. *Totiglobus*, Domke and Dornbos 2010); B: sediment resting, where the organism passively settles atop the substrate, relying upon substrate stability for support (i.e. *Crumillospongia*, Dornbos et al. 2005); C: sediment sticking, where the organism inserts their basal end directly in the substrate (i.e. *chancelloriids*, Kloss et al. 2009).

space on Proterozoic-style substrates. Numerous bivalves and echinoderms from the Maotianshan and Burgess faunas exhibit hard substrate attachment (Dornbos et al. 2005), and it should be at least considered that this strategy may not be informative for determining substrate conditions.

3.2 Substrates Associated with Cambrian Faunas

The close relationship between substrate conditions and benthic adaptive strategies allows for interpretations of paleoenvironmental conditions by identifying the style of adaptive strategy preferred by the associated metazoans. When metazoans are demonstrably preserved *in situ* direct comparisons may be made with sedimentary fabrics to interpreted substrate conditions, however this approach may be used even when metazoans are not preserved *in situ* (Dornbos et al. 2005) and are useful for tracking the progress of the agronomic revolution during the Cambrian even when sedimentary evidence of the original depositional environment may not be preserved (i.e. the Burgess Shale fauna). Further, unlike the multiple potential interpretations of sedimentary fabrics, the observations of metazoan morphology are incontrovertible: Proterozoic-style adaptations should only be found in Proterozoic-style substrates, and vice versa. Paleoecological analysis, when available, thus offers some advantages over ichno-sedimentary work.

Dornbos et al. (2005) used this approach for a study of the paleocommunities of the Maotianshan and Burgess Shales, shedding light onto the temporal progression of

the agronomic revolution during the early and middle Cambrian. The Maotianshan Shale, an early Cambrian (520-516Ma) unit that preserves an *in situ* BST fauna, exhibits extremely low levels of bioturbation (~ii1) and cohesive sedimentary fabrics suggestive of Proterozoic-style substrates (Dornbos et al. 2005; Kloss et al. 2009). The fauna itself contains a diverse sessile benthic community that overwhelmingly prefers morphological adaptations to Proterozoic-style substrates (89% of sessile benthic metazoans). Only two genera utilize Phanerozoic-style substrates: *Micromitra* and *Nisusia*, bivalves that are both hard substrate attachers (Dornbos et al. 2005). The Burgess Shale is a middle Cambrian (513-500Ma) unit and is the original BST fauna. Unlike the Maotianshan the Burgess Shale fauna is generally interpreted not to have been preserved *in situ* (although see Caron and Jackson 2008, and geochemical chapter), having been transported to the Burgess depositional setting from an adjacent shallow subtidal shelf via obrution events (Whittington 1985; Conway Morris 1986; Dornbos et al. 2005). The Burgess fauna includes numerous benthic metazoans that are the original “failed experiments” of Gould (1989) and is dominated by Proterozoic-style adaptive strategies, though not to the same abundance as found in the Maotianshan fauna (64%). Similar to the Maotianshan fauna the Burgess metazoans utilizing Phanerozoic-style substrates are bivalves, with the exception of the eocrinoid *Gogia*, and all are hard substrate attachers (Dornbos et al. 2005). Both localities preserve several genera with poorly constrained ecologies, rendering their adaptive strategies indeterminate (Dornbos et al. 2005). Based upon the decrease in abundance of Proterozoic-style adaptive strategies between the Maotianshan and Burgess faunas

Dornbos et al. (2005) concluded that Proterozoic-style substrates were in decline due to the effects of the agronomic revolution.

The above approach is modified here slightly in an attempt to quantify the association between substrate and metazoan adaptive strategy. The Substrate Adaptability Index (SAI) is a factor designed to give rough estimates of substrate dominance based upon the adaptive strategies of associated metazoans. SAI is simply:

$$\text{SAI} = \text{Ph}/\text{T},$$

where Ph is the total number of metazoans known to exhibit Phanerozoic-style substrate adaptations; and where T is the total number of sessile benthic metazoans with known adaptive strategies observed in the fauna. A SAI of 0.0 (no Phanerozoic-style adaptive strategies present) suggests dominance of Proterozoic-style substrates, whereas a SAI of 1.0 (all observed metazoans exhibit Phanerozoic-style adaptive strategies) suggest dominance of Phanerozoic-style substrates. Most Cambrian benthic communities will likely fall between the end members of this spectrum: the Maotianshan fauna has a SAI of 0.11 (2 Phanerozoic-style genera, 19 total) and the Burgess fauna has a SAI of 0.38 (8 Phanerozoic-style genera, 22 total). SAI presents itself as a useful metric because it allows for quick comparisons between disparate faunas-- the Maotianshan (0.11) clearly has greater association with Proterozoic-style substrates than the Burgess (0.38)—as well as providing a numerical value for use in graphical or statistical analysis. The SAI value may also be calculated using mobile benthic metazoans when their substrate preferences are reasonably well known (i.e. the mat grazer

Wiwaxia, or soft substrate infaunal burrowers like *Lingula*), as well as some trace fossils that would require soft substrates for their behavior (i.e. deposit feeding trace *Cruziana*).

It should also be noted that intermediate SAI values should not be considered as analogous to the relative dominance of substrate conditions, i.e. a SAI of 0.50 does not necessarily indicate that the environment was split evenly between Proterozoic- and Phanerozoic-style substrates. As noted previously the presence/absence of Proterozoic-style adaptive strategies is more significant than their Phanerozoic counterparts; and such considerations should be taken into account, in addition to other depositional and environmental factors, when evaluating SAI values.

3.3 SAI: Spence, Wheeler, and other BST Faunas

SAI was calculated for both the Spence and Wheeler Shale faunas, as well as numerous other BST faunas from the late Neoproterozoic-Cambrian period (Fig. 3.5), in order to determine the temporal and spatial effects of the agronomic revolution on a global scale. Data for the SAI calculation was collected as follows, in order of priority: 1) direct observations and interpretations of observed morphologies of fossil specimens from Spence and Wheeler Shale localities; 2) observations and interpretations of morphologies taken from published figures, illustrations, and plates of fossil specimens collected from the Spence and Wheeler Shales; 3) literature review of previously published ecological interpretations of fossil specimens from the Spence and Wheeler



Figure 3.5. Geographic distribution of Burgess Shale-type faunas utilized in the accompanying paleoecological study. 1- Mount Cap Formation; 2- Burgess Shale; 3- Spence Shale; 4- Wheeler Shale; 5- Marjum Formation; 6- Pioche Shale; 7- Chisholm Shale; 8- Indian Springs Lagerstätte; 9- Lantham Shale; 10- Kinzers Formation; 11- Parker Slate; 12- Sirius Passet; 13- Orsten; 14- Maotianshan Shale; 15- Emu Bay Shale; 16- Winnishiek Formation.

Shales; 4) literature review of previously published ecological interpretations of fossil genera known to occur in the Spence and Wheeler Shales (but interpretations not necessarily based upon observations of fossils from said shales); and 5) ecological data of fossil genera culled from the online Paleobiology Database (PDB). In some cases multiple lines of data were combined to best constrain the ecological interpretations of fossil specimens. While sessile benthic metazoans were the primary target of analysis and inclusion in the SAI calculation, the ecologies of associated of notable mobile benthic metazoans (i.e. *Wiwaxia*, monoplacophorans) were included where appropriate. Sessile benthic metazoans whose ecologies are poorly constrained were not included in the SAI calculation, although their presence was noted for potential inclusion at a later date when better paleoecological information becomes available. SAI values are reported as a measure of geologic time (Fig. 3.6; based upon the best constraints available).

The Spence Shale Fauna: 15 genera of sessile benthic metazoans were identified in the Spence Shale, with the majority of these specimens found in the Miner's Hollow and High Creek localities (Appendix 2). The ecologies of *Ctenocystis* and *Protospongia* are indeterminate. Seven genera exhibit Phanerozoic-style adaptive strategies: the hard substrate attaching lingulids *Acrothele*, *Dictyonina*, and the rhyconelliform *Diraphora*; the eocrinoid *Gogia*; the infaunal burrowing lingulids *Lingullela* and *Micromitra*; and the

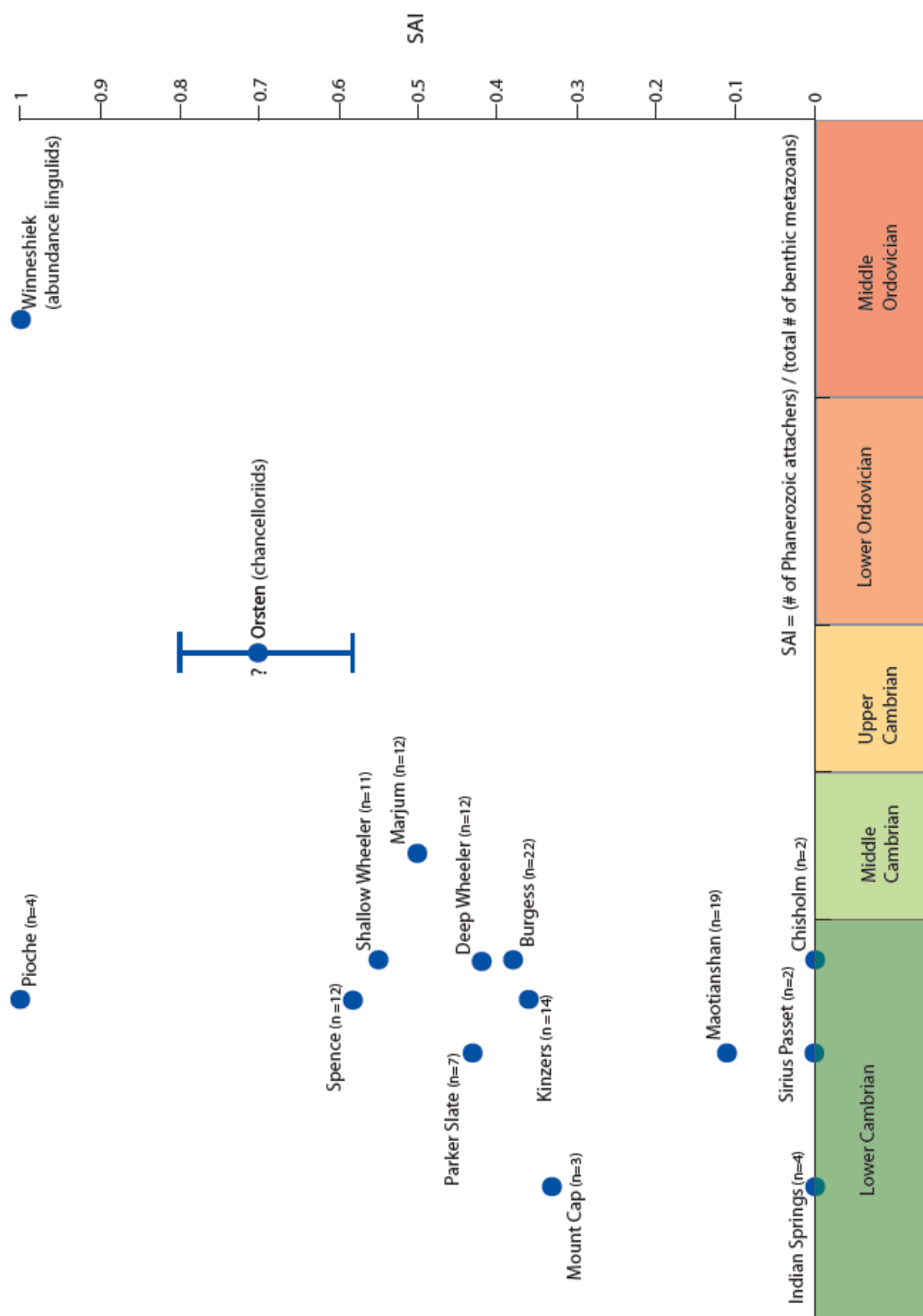


Figure 3.6. SAI values as a function of geologic time for numerous BST faunas and the exceptionally preserved Winneshiek Formation (control).

trace fossil *Cruziana*. Six genera exhibit Proterozoic-style adaptive strategies: the sediment resting sponges *Choia* and *Vauxia*, the mat grazing monoplacophoran *Scenella*, the mat grazer *Wiwaxia*, and the sediment sticking chancelloriids *Chancelloria* and *Allonnia*.

The presence of the genera *Gogia* and *Allonnia* here are noteworthy and merit further discussion. Eocrinoid morphology underwent significant developmental changes during the Cambrian substrate revolution, discarding the early primitive 'hohlwurzel' stem structures for 'true' echinoderm stems with ossicle plating in response to the agronomic revolution (Bottjer et al. 2000). Individual gogiid species may exhibit either Proterozoic- or Phanerozoic-style adaptive strategies; further, at least one species, *Gogia spiralis*, may change adaptive strategies during ontogeny (Schlottke 2008). The gogiid species identified in the Spence Shale developed true stems that suggest hard substrate attachment and are identified as such here; however, it must at least be considered that some individual specimens of *Gogia* may exhibit Proterozoic-style adaptations.

The genus *Allonnia* has not been previously described in the Spence Shale; however, one specimen of *Allonnia* was observed in the collection of amateur paleontologist Val Gunther of Brigham City, Utah during the 2009 field season (pers. obs.). Chancelloriid genera are notoriously difficult to identify, in part due to the sometimes confusing nature of their sclerite morphology, and this may explain the lack of previous identification of *Allonnia* in this unit (Janussen et al. 2002, Randell et al.

2004). The 3+0/2+0 sclerite morphology of the Gunther specimen definitively places the specimen with the genus *Allonnia* and distinguishes it from the typically 3+1/4+1 sclerite morphology of the more common *Chancelloria* (Fig. 3.7). Chancelloriids have been previously interpreted as sediment stickers (Dornbos et al. 2005; Kloss et al. 2009). Bengtson (2010) observed chancelloriid specimens attached to hard substrates in the Burgess Shale; however, an exhaustive study of more than 600 specimens of chancelloriid from the Maotianshan Shale found no evidence of hard substrate attachment among chancelloriids (Kloss et al. 2009), and none of the specimens observed from the Spence Shale exhibit adaptation or attachment to hard substrates.

The Spence's SAI value (0.54) suggests a relatively heterogeneous substrate. Phanerozoic-style substrates undoubtedly existed to support the behavior of *Lingulella* and *Micromitra*; yet there exists a significant contingent of Proterozoic-style adapted genera to suggest a robust population of Proterozoic-style substrates. The agronomic revolution was likely still in its early stages at the time represented by the Spence fauna, findings that are consistent with the ichnofabric analysis of the Spence Shale itself (~ii1).

The Wheeler Shale Fauna: Robison (1991) distinguishes between the subtidal shelf "shallow" Wheeler and that of the offshore "deep" Wheeler, a distinction based upon outdated paleoenvironmental interpretations (Halgedahl et al. 2009). However, there are subtle distinctions between the benthic genera of Robison's shallow and deep Wheeler units that may relate to small-scale differences in depositional conditions between the two units, and as such the two faunas are treated separately here.

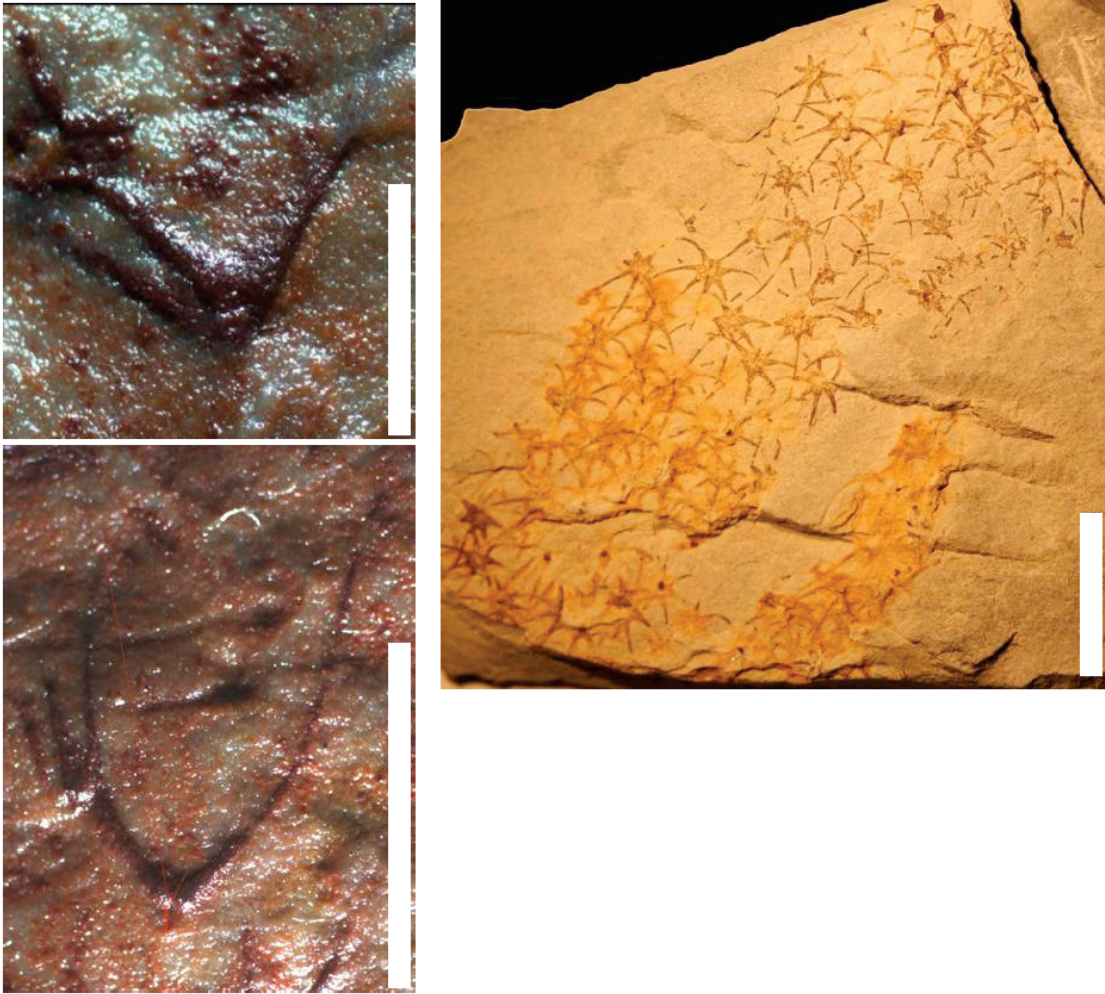


Figure 3.7. Left: 2+0/3+0 sclerites from a disarticulated specimen of *Allonnia* sp. from the Wheeler Amphitheatre. Above: Specimen of *Chancelloria eros*, also from the Wheeler Amphitheatre, with 4+1 and 5+1 sclerite morphology. Scale bars = 5mm.

The shallow Wheeler contains eleven benthic genera with well-constrained ecologies (Appendix 2). Five genera exhibit Proterozoic-style adaptive strategies split between sediment stickers and mat grazing mobile benthic metazoans. Unlike the Spence Shale fauna, *Gogia* is categorized here as a sediment sticker. The sole species of *Gogia* found in the Wheeler Shale is *G. spiralis*, which ontogenetically developed sediment sticking as a means of attachment during adulthood (Dornbos 2006, Schlottko 2008). *Latouchella* and *Pelagiella* are small, mm-scale helcionellid mollusks that are generally reconstructed as epifaunal grazers in the same vein as the superficially similar monoplacophorans (Berg-Madsen and Peel 1993; Parkhaev 2000; Atkins and Peel 2008). While never explicitly identified as mat grazers in systematic treatments, their general ecology, association with muddy substrates, and rather small size suggest that life would have been relatively difficult on Phanerozoic-style substrates where the presence of a mixed layer would prove a considerable barrier to a grazing habit (see Dornbos et al. 2005 discussion of the similarly diminutive lobopodians; but also see discussion of *Yochelcionella* below). The remaining six genera utilize Phanerozoic-style adaptive strategies that emphasize behaviors requiring soft substrates: *Acrothele* and *Lingullela* again are infaunal burrowers; *Treptichnus* is a deposit feeding trace fossil requiring soft sediment for the feeding behavior represented; and *Rusophycus* is a resting trace that would require soft sediments for preservation. Given the nature of both traces, *Treptichnus* and *Rusophycus* were likely contributing factors to Phanerozoic-style substrate development in the shallow Wheeler Shale. Paleoecological analysis is again

relatively consistent with ichnofabric analysis, suggesting relatively low bioturbation levels in the Wheeler.

Twelve benthic genera are well known from the deep Wheeler Shale unit, seven of which are either mat grazers or sediment stickers (Appendix 2). *Allonnia* is again identified here as occurring for the first time in the Wheeler Shale, with a single disarticulated specimen collected at the Wheeler Amphitheatre during the 2008 field season. This specimen, while poorly preserved, clearly exhibits the distinctive wishbone-shaped 3+0/2+0 sclerite morphology of the *Allonnia* genera, (Fig. 3.7) and again is classified among other cancelloriids as a sediment sticker. Phanerozoic-style adaptive strategies in the deep Wheeler are lacking both trace fossils *Treptichnus* and *Rusophycus* found in the shallow Wheeler units, although infaunal burrowing bivalves have a similarly robust presence here. The paleoecological data from the shallow Wheeler suggests an even stronger association with Proterozoic-style substrates than the shallow unit, again consistent with ichnofabric analyses.

Although the differences in SAI values for the shallow and deep Wheeler units are slight (0.55 vs. 0.42, respectively), a closer look at the benthic communities reveals that these small-scale differences are markers for tracking the agronomic revolution across changing depositional environments. The complex tracemaking behaviors represented by *Treptichnus* and *Rusophycus* are observed only in shallow subtidal shelf settings; and it is in these very same environments where diversity among Proterozoic-style adapters is also lower, compared to the deep Wheeler. Complex trace fossils first

have their origins in shallow settings, contemporaneous with the evolution of early metazoans making these traces, before migrating toward the outer shelf and into deeper marine environs (Bottjer et al. 1988; Jensen 2003; Seilacher et al. 2005). As complex tracemaking behavior migrated across the continental shelf, the agronomic revolution likely followed, and the differences observed between the shallow and deep Wheeler may represent a “snapshot” of the typical middle Cambrian shelf where complex burrowing behaviors had already escalated the agronomic revolution within shallow shelf settings but the same effect had yet to reach the deeper outer shelf, providing a more favorable habitat for metazoans utilizing Proterozoic-style adaptive strategies.

Other BST Faunas: The Marjum Formation is a carbonaceous shale overlying the Wheeler formation that also contains its own BST fauna as diverse as either the Spence or Wheeler Shales. Its fourteen benthic genera are split between Proterozoic- and Phanerozoic-style adapters. The Marjum fauna includes sediment stickers, sediment attachers, sediment resters, mat grazers, and the mat walking lobopodian *Aysheaia*. Among the Phanerozoic-style adaptive strategies present are two hard substrate attaching brachiopods and five infaunal burrowing genera, an increase in infaunal burrowers from the stratigraphically older Wheeler Shale and consistent with increasing burrower diversity and bioturbation intensity during the later stages of the agronomic revolution.

The Kinzers Formation of Pennsylvania is of equivalent age to the Wheeler Shale, and the fauna includes several unusual echinoderms unique to the formation.

Lepidocystis and *Kinzercystis* are eocrinoids that lack “true” crinoid-like stems with ossicles, instead bearing stem-like structures that are extensions of the aboral surface with irregular arrangement of the skeletal plates (Sprinkle 1973). As the stems lack obvious means of attachment to hard substrates or stabilization in the soft muddy substrates of the Kinzers formation, it is likely that both utilized sediment sticking for attachment. *Camptostroma* is an unusual medusoid-shaped echinoderm with either a flattened or slightly concave upward basal end (Durham 1966), suggestive either of a sediment resting or sediment attaching habit. *Planutenia*, *Pelagiella* and *Yochelcionella* are helcionellid mollusks with morphologies and ecological affinities suggestive of a mat grazing lifestyle. Atkins and Peel (2008) suggest that some distinctions in helcionellid ecology should be made based upon shell morphology for *Yochelcionella*, where more strongly curved shells may be indicative of a semi-infaunal deposit feeding habit, whereas conical or orthoconic shell designs are more typical of epifaunal grazers. The Kinzers formation preserves three species of *Yochelcionella* that exhibit both shell morphologies; however, it is the opinion of the author here, based upon the body of helcionellid literature available, their diminutive size and their association with muddy substrates that it is likely most helcionellids utilized a mat grazing lifestyle and are categorized accordingly. Phanerozoic-style adaptive strategies found in the Kinzers consist of two genera of hard substrate attaching brachiopod and three burrowing lingulids.

Other BST faunas surveyed—the Sirius Passet Formation, the Pioche Shale, the Chisholm Shale, the Latham Shale, the Mount Cap Formation, the Parker slate, and the Orsten assemblage—contain few known benthic genera and thus SAI values are skewed significantly. Taken as a whole these units have a heterogeneous assemblage of Proterozoic- and Phanerozoic-style adaptive strategies suggesting that intermediate heterogeneous substrate conditions were a global phenomenon during the early-to-middle Cambrian period.

In addition to the Cambrian BST faunas surveyed, two additional faunal assemblages were included as controls. These assemblages were chosen for two reasons: a) they occurred during a geologic period outside of the agronomic revolution, and thus their benthic assemblages should represent typical diversity found in environments where substrate conditions were homogeneous; and b) like the BST faunas these additional assemblages are Lagerstätten and thus the degree of preservational diversity (i.e. the apparent generic diversity of the assemblage based upon what is actually preserved and observable) most closely matches that of the Cambrian BST faunas. The pre-agronomic-revolution period is represented by the Mistaken Point Ediacaran assemblage located in Newfoundland. This assemblage includes twelve genera of Ediacaran soft-bodied metazoans that, through morphology or ecology, suggest affinities for Proterozoic-style substrates (Narbonne 1998, Clapham and Narbonne 2003; Tarhan et al. 2010; Wilby et al. 2011), giving the Mistaken Point assemblage a SAI of 0.0 as predicted by the agronomic revolution. Conversely, the Winneshiek Formation, a middle Ordovician unit found in Iowa, is known primarily for

its exceptional preservation of trilobites and other mobile arthropods (Liu et al. 2006). While other benthic fauna are scarce, lingulid brachiopods, an infaunal burrowing species, are known to be abundant (Liu et al. 2006), and the general ecology of trilobites and other early arthropods suggest that deposit feeding behaviors were likely also common. The Winneshiek Formation fauna is assigned a SAI of 1.0, again consistent with expectations from the agronomic revolution.

3.4 Discussion

A plot of SAI values through geologic time (Fig. 3.6) reveals that all Cambrian BST faunas exhibit some evidence for heterogeneous substrate conditions, though the degree of heterogeneity and the relative abundance of Proterozoic-versus-Phanerozoic-style substrates varies considerably. The agronomic revolution was a geologically synchronous global event that is restricted to the Cambrian period, whereas before and after the agronomic revolution benthic faunas demonstrate affinities for homogeneous substrate conditions (SAI: 0.0, 1.0). There is no discernible pattern regarding the progression of the agronomic revolution from the early to middle Cambrian (SAI: 0.11-0.58 for faunas with genera $n > 7$).

It is possible that environmental factors played a role in controlling the progression of the agronomic revolution, and differences between depositional conditions associated with BST faunas contributed to varying rates of substrate turnover during the Cambrian. Paleoenvironmental conditions are known to have affected

patterns of distribution of fossil organisms, i.e. onshore-offshore trending (Jablonski et al. 1983; Bottjer et al. 1988), bathymetry (Ekdale 1988), environmental gradients (Frey et al. 1990), and local transient changes in physical or chemical conditions such as a fluctuating oxycline (Brett et al. 2009) or salinity (Babcock 2001). BST faunas are remarkable in the sense that their similarities in method of fossil preservation occur under disparate depositional conditions. The Burgess Shale fauna was located in deep water at the base of a carbonate reef shelf where occasional slumping or turbidity events transported the organisms further downslope for eventual burial and preservation (Whittington 1985, Conway Morris 1986). This environment may be compared to the deep Wheeler, which was found along the outer shelf of the House Range Embayment (Rees 1986). In contrast to these deep water environs the Chengjiang fauna is found in a shallow water shelf within a restricted basin subject to fluctuations in salinity (Babcock 2001), and the Emu Bay Shale was deposited in relatively shallow waters within the photic zone under an oxic water column (McKirdy et al. 2011). This disparity in depositional conditions may explain in part the lack of linear progression of the agronomic revolution when viewed from the SAI data. Environmental factors may also explain observations made within the faunas themselves: the greater diversity of trace fossils in the shallow Wheeler fauna compared to the deeper Wheeler fauna may be indicative of onshore-offshore trending, with increased infaunal activity affecting the diversity of Proterozoic-style adapters (see discussion of the Wheeler Shale fauna above). It may also serve to explain why the deep water Burgess Shale, though one of

the youngest BST faunas, still preserves a remarkably diverse Proterozoic-style adapted fauna.

It is also important to consider that the range of SAI values results from small sample sizes. Only the benthic faunas of the Maotianshan and Burgess Shales include more than 15 genera with determinate adaptive strategies (n=19, 22 respectively). Differences in relative abundances of Proterozoic-vs.-Phanerozoic adaptive strategies between Cambrian faunas are not statistically significant. Thus, the variability in SAI values between temporally coeval faunas may not be ecologically informative. However, that does not diminish the significance of the paleoecological analysis presented here. While we may not be able to place too much stock into comparisons of the slight differences in SAI value between BST faunas, the mere presence of both Proterozoic- and Phanerozoic-style adaptive fauna in many of these localities indicates that heterogeneity of the substrate was widespread during the early-middle Cambrian; that nonactualistic substrates were still an important physical control on depositional environments; and, considering the number of Proterozoic-style adapted fauna observed at these localities, that nonactualistic substrates were still influential in the morphological development of benthic fauna until at least late Cambrian time.

It should also be considered that SAI values may be limited to the relative “flexibility” of Proterozoic-vs.-Phanerozoic-style adaptations. The morphology of Proterozoic-style adaptive strategies would make it very difficult for these adaptations to be effectively utilized on Phanerozoic-style substrates: Proterozoic-style adaptive

strategies are “rigid” and their presence is a sure signature of Proterozoic-style substrates. Conversely the morphology of Phanerozoic-style adaptive strategies suggest that they could be successfully adapted to Proterozoic-style substrates under the proper conditions, i.e. the presence of hardgrounds or appropriate skeletal material for attachment by hard substrate attachers. Phanerozoic-style adaptations are “flexible” and therefore their abundance within BST faunas is not as strong an indicator of the relative abundance of Phanerozoic-style substrates. The relative abundance of Proterozoic-style substrates is likely underestimated using a metric like SAI.

In depositional settings where the burial environment is not the *in situ* environment where the fauna was living, the use of paleoecological analysis is the only practical method of establishing the nature of the *in situ* substrate. Such is the case of for the Burgess Shale: it is well established that the fauna preserved within the Burgess Shale was transported downslope from its point of origin adjacent to a reef shelf (Whittington 1985; Conway Morris 1986). The preservational environment of the Burgess Shale fauna is not coincident with its *in situ* environment and therefore any sedimentological or ichnofabric analysis of the Burgess Shale itself provides no ecological value in regards to the preserved faunal community. In such a case paleoecological analysis provides a significant advantage over ichnological or geochemical analyses.

3.5 Conclusions

The paleoecological analysis of BST faunas presented here demonstrates that:

- 1) Proterozoic-style adaptive strategies are observed in nearly all Cambrian shales where Burgess-Shale-type faunas are preserved.
- 2) Phanerozoic-style adaptive strategies are also observed in Cambrian shales in association with Proterozoic-style strategies.
- 3) The association of both Proterozoic-and-Phanerozoic-style adaptations in BST faunas suggests a mixing of both Proterozoic-and-Phanerozoic style substrates in Cambrian settings in accordance with the agronomic revolution.
- 4) The agronomic revolution was a global event that allowed for the development of unique marine communities that are not observed outside of the Cambrian period.
- 5) The Substrate Adaptability Index (SAI) is only a rough measure of the relative mixing of Proterozoic-vs.-Phanerozoic-style substrates, with values affected by sample size, depositional environment, and the flexibility of Phanerozoic-style adaptations (i.e. Phanerozoic-style adaptations may be effectively employed in Proterozoic-style environs).
- 6) Paleoecological analysis is informative when connections between burial environment and *in situ* environment cannot be established.

CHAPTER 4: GEOCHEMICAL PROXIES FOR REDOX AND ENVIRONMENTAL CONDITIONS

Recent geochemical data of several Cambrian marine shales (Powell et al. 2003; Powell 2009; McKirdy et al. 2011) reveal that these depositional settings were typified by dysoxic to fully oxygenated waters, in stark contrast to traditional interpretations based on ichnofabrics. The sample geochemical techniques are applied here to the Spence, Wheeler, and Maotianshan Shales to determine the redox conditions associated with the deposition of these units. XRF analysis of four redox-sensitive elements—V, Cr, Ni, and Zn—was carried out and redox conditions estimated using the paleoredox indices (PI) V/Cr and $V/(V+Ni)$ and enrichment factors (EF). PIs suggest generally oxic bottom waters were present in all three shale units. EF of V for the Spence and Wheeler are significantly depleted with respect to the World Shale Average (WSA; Wedepohl 1991) suggestive of well-oxygenated conditions. A lack of Ni enrichment suggests that depositional conditions were not reducing, consistent with interpretations of V. Zn is slightly to significantly enriched in both the Spence and Wheeler Shales; this may indicate that the oxic-anoxic boundary is very close to or at the sediment-water interface (Calvert and Pedersen 1993). The Maotianshan Shale appears to be more dysoxic than either the Spence or Wheeler Shales. The presence of slightly oxic to well-oxygenated waters in all three shales is a reversal of traditional interpretations of dysoxic-to-anoxic conditions in the Spence, Wheeler, and Maotianshan Shales based upon ichnofabric analysis. The decoupling of redox conditions with bioturbation

supports the hypothesis that Proterozoic-style substrates were present in all three shales. The presence of oxygenated conditions in many Cambrian marine shales poses challenges for understanding the mechanisms involved in BST preservation, which generally assumed the presence of anoxia (Gaines and Droser 2010). It is possible that the presence of microbial mats in association with Proterozoic-style substrates may have facilitated exceptional fossil preservation in well-oxygenated Cambrian environments.

4.1 The Agronomic Revolution and Redox Conditions

The Spence, Wheeler, and Maotianshan Shales were deposited at a critical time in both animal and marine environment evolution. The emergence of modern animal phyla and modern animal behaviors would leave a lasting mark on marine ecosystems through the rest of the Phanerozoic. The diversification of burrowing organisms and increasing complexity and tiering depth of trace fossils resulted in thoroughly mixed substrates with high water contents quite unlike the earlier Proterozoic-style firmgrounds (Seilacher and Pflüger 1994). The Phanerozoic-style substrates born from this so-called agronomic revolution (Seilacher and Pflüger 1994) would come to dominate marine settings until the present day (see Thayer's [1979, 1983] modern exploration of marine substrates).

Immobile benthic metazoans adapt various morphological strategies for stability on a given substrate, and these strategies are tailored to substrate conditions (see

previous chapters). As substrate conditions changed during the agronomic revolution, these organisms in turn were forced to evolve and adapt new morphologies in order to compensate and maintain their position on the seafloor (Bottjer et al. 2000). This event, the Cambrian Substrate Revolution (CSR), has been widely identified in studies of early Cambrian benthic metazoan morphologies (McIlroy and Logan 1999; Bottjer et al. 2000; Parsley and Prokop 2004; Dornbos et. al. 2005; Dornbos 2006; Domke and Dornbos 2010) and its recognition is significant for our understanding of the unique faunal menagerie associated with the Cambrian Radiation (Gould 1989).

The Spence and Wheeler Shales are early-middle Cambrian sedimentary formations that preserved Burgess Shale Type (BST) Lagerstätte benthic communities of similar diversity to that of the more well-known Burgess and Maotianshan Shale faunas (see previous chapter), but have had only minimal attention given to the study of their role in recording the agronomic revolution and CSR (see Schlottke 2008). Greater attention has been given to paleoenvironmental setting and taphonomic conditions (Rees 1986; Gaines and Droser 2003; Gaines et al. 2005; Garson et al. 2008; Brett et al. 2009; Gaines and Droser 2010; Gaines et al. 2012). Based upon fossil evidence Gaines et al. (2005) described the Wheeler Shale BST faunal layers as being deposited under a fluctuating oxycline with redox conditions variable between dysoxic-to-anoxic, and interpreted this as a potential factor in BST preservation within the Wheeler fauna. Gaines and Droser (2003) further identified the trilobite *Elrathia kingii* as an exaerobic zone inhabitant, living in monospecific assemblages on minimally bioturbated (ii1) substrates. Substrate conditions above and below the *E. kingii* beds show increased

amounts of bioturbation (ii2-ii3) that Gaines and Droser (2003) interpret as increasingly oxic bottom waters. Note that the ichnofabric indices recorded in these beds are not suggestive of the development of a mixed layer or Phanerozoic-style substrates (Droser and Bottjer 1986). Brett et al. (2009), building off of the fluctuating oxycline model of Gaines et al. (2005), interpreted the minimally bioturbated (ii1) Wheeler Shale beds as representative of deposition under anoxic bottom waters. From their data and interpretations it likely that these workers assume the dominance of Phanerozoic-style substrates in the Wheeler Shale. Handle and Powell (2010) presented geochemical data indicating that redox conditions were variable between anoxic and oxic in the fossiliferous strata of the Wheeler Shale, generally confirming Gaines et al. (2005) fluctuating oxycline model. Handle and Powell's analysis did not address how these fluctuations in redox correlated to bioturbation or putative substrate conditions. Finally, Garson et al. (2008) utilized ichnofabric analysis to demonstrate that the Spence Shale was generally deposited under dysoxic-to-anoxic conditions, invoking a fluctuating oxycline model similar to that proposed for the Wheeler Shale. It is likely that Garson et al. (2008) is referring to Phanerozoic-style substrates when making their interpretations.

Based upon paleoecological information, it is likely that Proterozoic-style substrates must have existed as some fraction of the substrate environment in the Spence, Wheeler, and Maotianshan Shales (see previous chapter). The consideration of substrate conditions is critical to proper interpretations of paleoenvironment and for understanding the association between ichnofabric indices and redox conditions. From the recent work of Gaines and Droser (2010), Brett, et al. (2009), and the work

presented in preceding chapters, it is clear that similar batches of data are revealing differences in interpretation based upon the expected presence of substrate conditions; and the addition of paleoecological data, while informative about substrate expectations, does not definitively establish the presence nor abundance of Proterozoic-style substrates in either the Spence or Wheeler Shale. Another approach, or rather, combination of approaches, would be helpful in clearing up the confusion.

Here such an approach is taken: a combination of geochemical, ichnological, and paleoecological models is applied to sedimentary materials from the Spence and Wheeler Shales to determine if, and to what extent, Proterozoic-style substrates existed in these depositional environments. Geochemical redox proxies are utilized to measure the nature of bottom water redox conditions at the time of deposition. These models have the advantage of being applied independent of substrate conditions, and in concert with ichnofabric and paleoecological analysis should be able to effectively evaluate the hypothesis that ichnofabric and paleoecological observations made in the Spence and Wheeler Shales support the presence of Proterozoic-style substrates in these depositional environments.

4.2 Redox Conditions and Faunal Activity

All metazoans require oxygen for respiration. The availability of dissolved oxygen in marine waters is an important control to the size, distribution, and behavior of animals in benthic environments (Rhoads and Morse 1971; Savrda and Bottjer 1986;

Ekdale and Mason 1988). Differences in metazoan activity levels are discernible at measurable thresholds in dissolved oxygen content (DOC), and are categorized into one of three “zones”: the aerobic (well oxygenated) zone where environmental DOC is >1.0 mL O₂/L H₂O; the dysaerobic (poorly oxygenated) zone where environmental DOC is between 0.1-1.0 mL O₂/L H₂O; and the anaerobic (no oxygen) zone where environmental DOC is <0.1 mL O₂/L H₂O (Rhoads and Morse 1971; Savrda et al. 1984; Ekdale and Mason 1988). Savrda and Bottjer (1987) added a fourth category, the exaerobic zone, which occurs at the dysaerobic/aerobic boundary with low oxygen levels (DOC 0.1-0.2 mL O₂/L H₂O) and unusual occurrences of macroscopic benthic fauna. Studies of modern low oxygen marine basins (Rhoads and Morse 1971; Savrda et al. 1984) have demonstrated correlations between diversity and density of both macrofauna and ichnofauna and oxygenation levels. Trace fossils models have proven to be reliable indicators of paleo-oxygen conditions (Savrda and Bottjer 1986; Ekdale and Mason 1988), and are commonly used to interpret paleoenvironmental conditions in Cambrian shales: low-to-no oxygen environments evidenced by abundant laminated sediments and rare, diminutive trace fossils (Rees 1986; Gaines and Droser 2003; Gaines et al. 2003; Garson et al. 2008, among others).

Complications arise when applying trace fossil models to Cambrian shales due to the likely presence of Proterozoic-style substrates, since these substrates 1) lack a well-developed mixed layer, leading to substrates with low water contents and in turn increasing the shear strength of the substrate, making it more difficult for burrowing organisms to disturb sediments (Savrda and Ozalas 1993; Seilacher and Pflüger 1994;

Bottjer et al. 2000; McIlroy and Logan 1999), and 2) were likely accompanied by layered microbial mats, which were instrumental in controlling redox conditions in the infaunal realm and possibly at the water-sediment interface (McIlroy and Logan 1999; Bailey et al. 2006). Microbial mats can rapidly exhaust supplies of available oxygen near the mat surface, resulting in anoxic conditions only a few millimeters beneath the surface, and occasionally anoxia may reach the surface or extend into the overlying water column (Froelich et al 1979; Bender and Heggie 1984; McIlroy and Logan 1999; Bailey et al. 2006). The presence of sulfate-reducing bacteria within the mat would have also led to the production of hydrogen sulfide (H_2S) within the subsurface, which is toxic to most animals and would have likely limited burrowing to organisms that have adapted means to tolerate high H_2S levels (Bailey et al. 2006). Thus, one might expect Proterozoic-style substrates to exhibit low bioturbation levels and a lack of trace fossils regardless of marine bottom water oxygenation.

The possible presence of Proterozoic-style substrates in Cambrian environments has not been appreciated in trace fossil studies of paleo-oxygen levels in Cambrian shales (Rees 1986; Gaines and Droser 2003; Garson et al. 2008). Rees (1986) interprets all shales from the House Range as being deposited under anoxic conditions, citing laminated sediments, the lack of infauna, and a dearth of shelly epifauna. The work of Gaines et al. (2003) support this interpretation, while Gaines and Droser (2003) suggest that the Wheeler Shale might better be characterized by the presence of an exaerobic zone. The observations made by Rees (1986) and later workers, however, could also be explained by the presence of Proterozoic-style substrates, which by definition would

lack significant bioturbation or the presence of infaunal organisms regardless of bottom water oxygen levels (Seilacher and Pflüger 1994; Bottjer et al. 2000). Rees (1986) explained the occurrence of rare shelly fossils (i.e. brachiopods, mollusks, sponges, etc.) as part of an allochthonous assemblage transported basinward during storm events; but not all fossil species found in the Wheeler Shale were deposited via transport. Gaines and Droser (2003) determined that *Elrathia kingii* was preserved *in situ*. The occurrence of many well-articulated specimens of the eocrinoid *Gogia spiralis* also suggests either *in situ* preservation via obrution events or minimal transport prior to burial, as eocrinoids easily disarticulate upon death (Brett et al. 1997). Mark Schlottke noted several possible *G. spiralis* preserved upright, in life position, on a slab recovered from the Wheeler Amphitheatre (Schlottke 2007). It is also likely that *Chancelloria eros* was preserved *in situ* or buried with minimal transport (pers. obs.).

Garson et al. (2008) came to similar conclusions regarding the paleoenvironment of the Spence Shale, suggesting that the laminated mudstones in which BST preservation occurred was anoxic, though they note that occasional periods of dysoxia were necessary to support the assemblage of shelly fauna. The Spence Shale biota is diverse (Liddell et al. 1997, but also see Q1 above) which is atypical of dysaerobic environments where low diversity or monospecific assemblages dominate but is more typical of aerobic conditions (Savrda and Bottjer 1986; Ekdale and Mason 1988). The presence of Proterozoic-style substrates could explain both the laminated sediments and the diverse biota.

Interpretations of the Maotianshan Shale that suggest the dominance of Proterozoic-style substrates have been criticized, mostly because of a lack of evidence for microbial mats on the substrate (Schieber 1999; Dornbos et al. 2005; Kloss et al. 2009). However, the presence of microbial mats is only one criterion for Proterozoic-style substrates, and laminated strata and the lack of a mixed layer still speak strongly for current models of the Maotianshan Shale substrate. This highlights the difficulty in assessing depositional environments where non-actualistic substrates may have been present.

4.3 Geochemical Proxies for Redox Conditions in Marine Settings

Marine waters are planetary-scale Ehrlenmeyer flasks where countless geochemical reactions take place from one moment to the next. The elemental materials involved in these reactions have multiple provenances (Fig. 4.1): terrigenous or *detrital* material derived from the erosion and transport of continental materials; *biogenic* materials derived either through creation or destruction from biological processes; *hydrothermal* material extruded from marine volcanism; and dissolved *authigenic* material present in marine water. The authigenic fraction includes multiple minor and trace elements that exist in multiple valence states and solubilities in ocean water, and the relative abundances of different valences for a given element are controlled by redox conditions. For example, Vanadium (V) has two primary oxidation states, V(V) and V(IV), and a lesser oxidation state, V(III) (Calvert and Pedersen 1993;

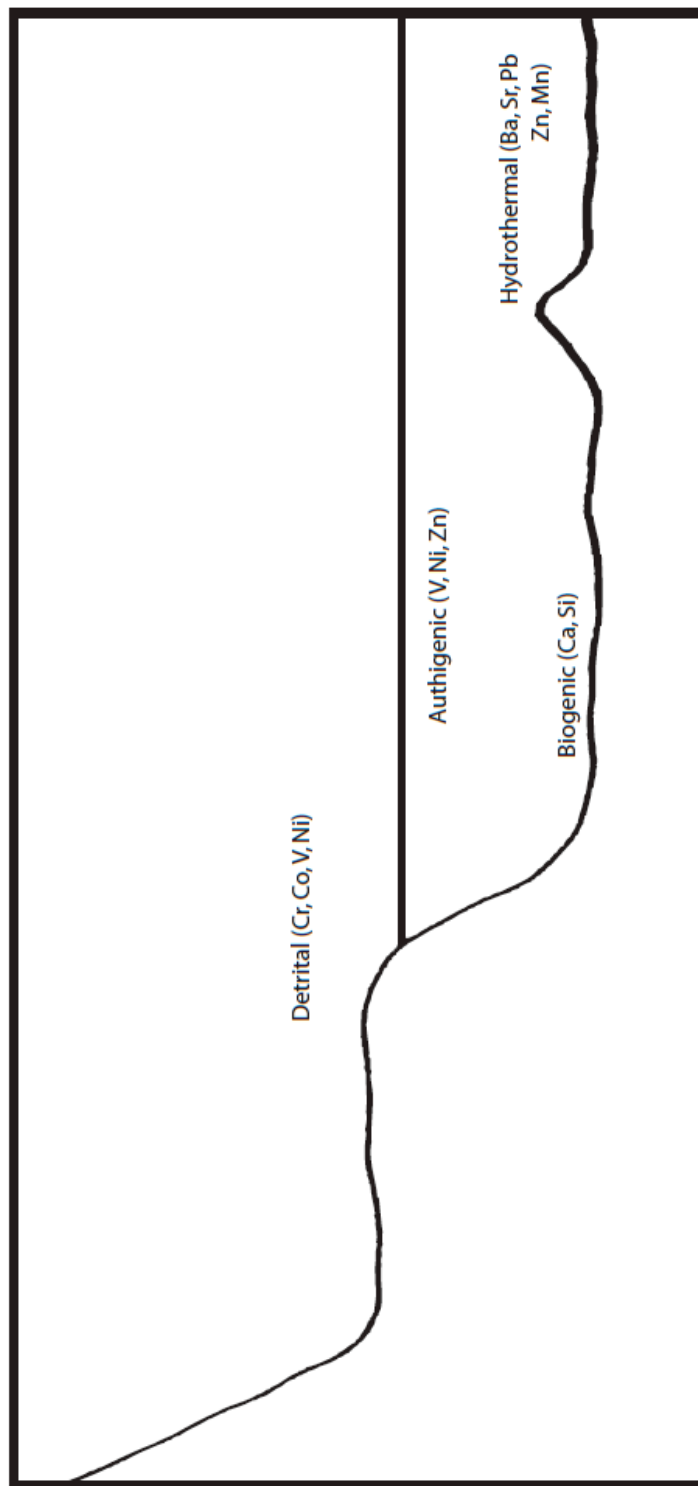


Figure 4.1. Potential sources for minor and trace elements found in seawater. Data collected from Tribovillard (2006) and Piper and Calvert (2009).

Tribovillard 2006). The V(V) oxidation state is stable under oxic conditions, and is relatively soluble (Fig. 4.2a); the V(IV) oxidation state is stable under reducing conditions, and is relatively insoluble, forming a hydroxyl precipitate or directly adsorbing to the sediment surface (Fig. 4.2b). V(IV) may be further reduced to V(III) under reducing, sulfidic conditions (Calvert and Pedersen 1993). Sediments deposited under oxic conditions should exhibit relatively little accumulation of V, while most remains dissolved within the overlying bottom water; and sediments deposited under increasingly anoxic conditions should exhibit increasing concentrations of V as part of the solid component of the sediment, with very little dissolved V found in the overlying bottom water (Fig. 4.2). Elements whose valence state is affected by changing redox conditions include Cr, Mn, Mo, U, and V (Calvert and Pederson 1993; Tribovillard 2006). In addition to changing valence states in response to redox conditions, several elements retain their valence states while still being affected by paleoenvironmental conditions related to oxygenation. Cd, Cu, Ni, and Zn are found as a fraction of the dissolved solids in seawater, but are increasingly depleted in seawater as they transition from oxic surface waters to anoxic, sulfide-rich deep water basins (Calvert and Pederson 1993) where the elements are precipitated as metal sulfides.

The sensitivity of minor and trace elements to redox conditions has long been utilized by geochemists for interpretations of paleoenvironment during the deposition of organic-rich (i.e. black) shales (Demaison and Moore 1980; Dypvik 1984; Calvert 1987;

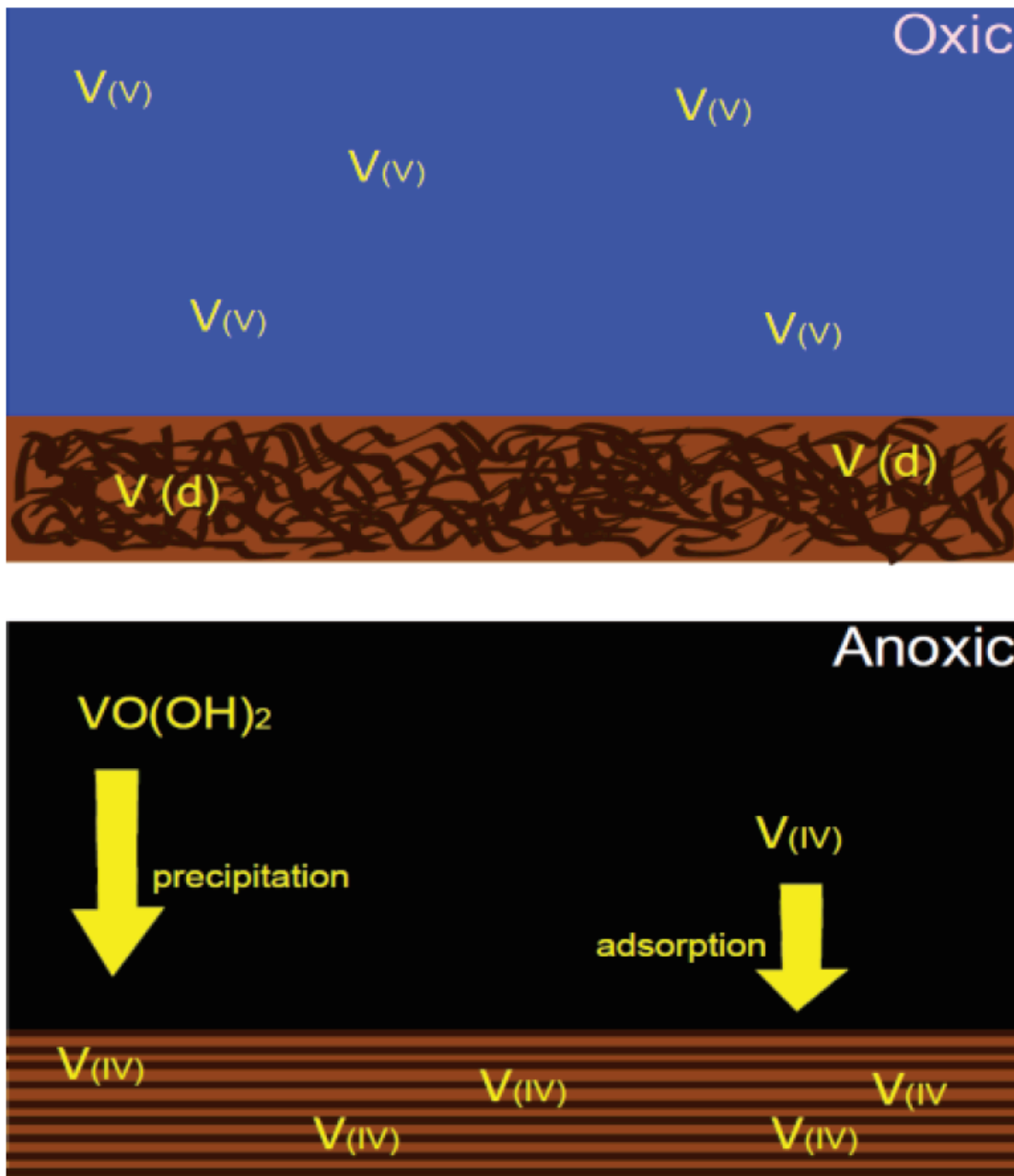


Figure 4.2. Accumulation of redox-sensitive element vanadium under both oxic and anoxic conditions. Top: Vanadium is found in the $V(V)$ oxidation state and is soluble under oxic conditions. Accumulation of vanadium in sediments is limited to the detrital fraction delivered via weathering. Bottom: Vanadium is reduced to $V(IV)$ under anoxic conditions. $V(IV)$ is delivered to the sediment either through precipitation or adsorption.

Jones and Manning 1994). Analysis is carried out using two primary methods: 1) direct comparisons of sample elemental concentrations versus standard concentrations from a calculated average (such as the World Shale Average provided by Wedepohl 1991); and 2) the generation of elemental ratios calibrated to detect changes in redox conditions (Jones and Manning 1994). Both approaches have been utilized in many analyses of Cambrian shale paleoenvironments (Schovsbo 2001; Powell et al. 2003; Powell 2009; Chang et al. 2009; Zhou and Jiang 2009; McKirdy et al. 2011). It must be noted that in both approaches the results are *proxies* for actual redox conditions, and are not direct measurements of dissolved oxygen concentrations (Tribovillard 2006).

Since trace elements act as redox proxies, it is important to consider how chemical and geological conditions beyond DOC may affect the elemental abundances preserved in Cambrian shales. The geochemical behavior of redox sensitive elements allows for their accumulation in sediments deposited beneath anoxic bottom waters; their precipitation may also occur *within* sediments, especially at increasing depth where anoxia predominates, as trace elements are precipitated from pore water (Calvert and Pedersen 1993). Because redox-sensitive elements can be precipitated both from anoxic bottom waters, but from also anoxic subsurface sediments regardless of the overlying bottom water conditions, then only the absence of enrichments provides a reliable indicator of overlying bottom water conditions (i.e. oxic bottom waters). Enrichment of redox-sensitive elements cannot distinguish reliably between anoxia in the bottom water versus the sediment (Calvert and Pedersen 1993). Paleoredox indices, however, are calibrated to allow for estimates of bottom water anoxia (Jones and

Manning 1994). Mn is the only reliable indicator for both oxic and anoxic bottom waters based upon its presence in modern sediments (Calvert and Pedersen 1993); however, Tribovillard (2006) counters that the mobility of Mn in reducing sediments allows for diffusion of Mn back into the overlying water column, thus making it an unreliable paleoredox proxy.

Remobilization of precipitated trace elements due to postdepositional re-oxygenation of sediments could lead to erroneous measurements of elemental concentrations. In general the oxidation of organic matter by bacteria in subsurface sediments leads to irreversible development of anoxic conditions (Tribovillard 2006). However, re-oxygenation is possible under particular circumstances, notably during abrupt changes in environmental conditions, i.e. rapid deposition associated with turbidites or obrution deposits (Thomson et al. 1998; Rinna et al. 2002). Obrution events have been noted in both the Wheeler and Spence Shales (Liddell et al. 1997; Brett et al. 2009) and the possibility of remobilization of trace elements via re-oxygenation exists. However, studies of modern marine sediment indicates that most redox-sensitive trace elements (with the exception of U) are fairly recalcitrant to re-oxygenation events, and those that do mobilize only migrate a short distance (<5cm) (Thomson et al. 1998). As the trace element analysis conducted here was measured on a 5-cm-scale, any effect of migration on elemental concentrations is likely insignificant.

Two approaches to measuring paleoredox, enrichment factors (EF) and paleoredox indices: Enrichment factors measure the relative enrichment or depletion of

an element with respect to a standard. EFs are also normalized with respect to Al (or Ti) help compensate for the detrital fraction present in each sample. A typical calculation of EF looks like this:

$$EF = (X_{sample}/Y_{sample})/(X_{standard}/Y_{standard})$$

Where X is the redox-sensitive element in question; and Y is the non-redox-sensitive element for standardization. Aluminum is the element used here, as most Al present in marine substrates is of terrigenous origin, and since Al is not redox-sensitive (Tribovillard 2006).

EF = 1 indicates elemental enrichment indistinguishable from that of the standard; EF >1 indicates enrichment of the element with respect to the standard, suggestive of increasingly anoxic conditions where dissolved solids would accumulate onto sediment surfaces; and EF <1 indicates depletion of the element with respect to the standard, suggestive of increasingly oxic conditions where the element remains soluble within the overlying bottom water. EFs cannot determine the extent to which waters are oxic or anoxic, or provide definitive measures of DOC. The standard used here is the World Shale Average (WSA) from Wedepohl (1991).

Paleoredox indices are ratios or formulas for concentrations of two or more redox-sensitive elements; this ratio number, or index, is then compared to a calibrated scale to determine redox conditions. Paleoredox indices operate with the knowledge that no two redox-sensitive elements react in the same way to changing redox conditions, although their response is predictable and repeatable; thus regular changes

in redox can be reliably determined (Jones and Manning 1994; Powell et al. 2003). Take, for instance, the ratio between the trace elements V and Cr, which is commonly recognized to be a reliable proxy for paleoredox conditions (Ernst 1970; Jones and Manning 1994; Scheffler et al. 2006; Powell 2009; McKirdy et al. 2011). In aerobic environments V is relatively soluble, but is relatively insoluble under reducing conditions (Sadiq 1988 via Scheffler et al. 2006). Cr is also relatively soluble in aerobic environments but less so in reducing environments (Scheffler et al. 2006). Since the reduction of V occurs at lower oxygen levels than Cr, comparing ratios of V/Cr in sedimentary materials is a useful proxy for paleoredox conditions (Jones and Manning 1994; Scheffler et al. 2006). V/Cr ratios less than 2 are indicative of aerobic environments; ratios between 2 and 4.25 indicate dysaerobic environments; and values above 4.25 are indicative of anaerobic conditions (Jones and Manning 1994; Scheffler et al. 2006).

4.4 Methodology

Samples for this study were collected over several field seasons during 2008, 2009, and 2010. 1.7m of strata of the Wheeler Shale were collected from the Antelope springs locality in Utah in 2008 and 2009. Approximately 4.0m of strata of the Spence Shale were collected from multiple localities in Idaho and Utah—Miner's Hollow, Oneida Narrows, and High Creek—during 2010. Material was excavated by pickaxe and chisel. Where possible material was chosen that exhibited minimal weathering. Strata were

sampled continuously upsection; however, weathering prevented sampling a complete section of either shale, thus the strata will be presented as “composite” sections. For Miner’s Hollow care was taken to sample localities corresponding to the parasequences of Liddell et al. (1997) in order to compare the results of this study with previous paleoenvironmental interpretations.

Immediately after excavation samples were wrapped in a protective layer of duct tape to prevent destruction during transport and later lab work. Once at the lab samples were sectioned perpendicular to bedding using a sedimentary rock saw. Part of the sample was retained for use for ichnofabric analysis, while the rest utilized for geochemical study. In addition to newly collected material, samples from previous work conducted in the Maotianshan Shale were utilized for the geochemical portion of this analysis. A total of 96 samples-- 34 samples from three localities in the Wheeler Shale, 57 from four localities in the Spence Shale, and 5 samples for a single locality in the Maotianshan Shale-- were prepared for analysis using a Bruker S4 Pioneer X-ray Fluorescence (XRF) Spectrometer by powdering each sample via an alumina shatterbox, and then fusing each into a glass beads using a fluxer. Glass beads were prepared with a 10:1 ratio of 50:50 LiM:LiT flux:sample (with LiBr as a non-wetting agent). Samples were analyzed via XRF using the same methodology as McHenry (2009). Each sample represents ~5cm of strata (5cm +/- 1cm). Strata from the Spence Shale series LMH2 was sampled at two intensities: one at ~5cm scale, and another at ~1cm scale. This was done to test the hypothesis proposed by Gaines et al. (2010) that the scaling intensity (i.e. m-scale) of geochemical analysis was not accurately portraying bed (mm-to-cm) scale

variations in redox conditions in Cambrian shales. Concentrations of V, Ni, Cr, and Zn were normalized for paleoredox analysis through both calculations for enrichment factors (EF; Tribovillard et al. 2006) and by the use of paleoredox indices V/Cr and V/(V+Ni) (Jones and Manning 1994; Schovsbo 2001). These trace metals and indices were selected because they could be detected and measured by XRF, as well as their common use and reliability found in the literature (Jones and Manning 1994; Schovsbo 2001; Powell et al. 2003; Tribovillard et al. 2006; Zhou and Jiang 2009). The geochemical results for V, Ni, Cr, and Zn (using EF) and V/Cr and V/(V+Ni) were analyzed using the techniques described above. These trace elements were chosen due to their redox-sensitivity, common appearance in paleoredox and geochemical analyses of marine shales (Calvert and Pedersen 1993; Jones and Manning 1994; Powell et al. 2003; Powell 2009; Zhou and Jiang 2009, McKirdy et al. 2011) and the lower limits of detection imposed by equipment and calibration procedures (i.e. other common redox-sensitive elements, such as U and Mo, were not part of the calibration and likely would not have been detectable using this technology) (McHenry 2008).

Previously recorded ichnofabric data from the Wheeler and Spence Shale were compared to geochemical data. The geochemical data from the Maotianshan Shale could not be correlated to previous sedimentological data, and is presented here without such context. While ichnofabric analysis was carried out at the millimeter scale, geochemical analysis was mostly limited to 5cm-increments because of methodological constraints. Aside from the section sample ~1-cm intervals, the comparison here does not offer a direct correlation between ichnofabrics and paleoredox, but rather offers

average paleoredox conditions over a period of deposition represented by the ichnofabric data. While not an ideal comparison, it remains generally informative of the relationship between substrate and paleoredox conditions.

4.5 Results

Complete results for the redox-sensitive elements analyzed by XRF are given in Appendix C. Additional redox-sensitive elements (i.e. U, Mo, etc.) were not analyzed during analysis or were detected at concentrations below the lower limits of detection for the XRF. V is reported with statistical error <12%; all other elements reported have statistical errors <10%. Elements are only reported if their concentrations exceed the Lower Limit of Detection (LLD) by at least twice. Overall *ii*-values are very low (average *ii* ~1) through sections in both shales (see previous chapter), with rare developments of minimal to moderate bioturbation (*ii*2-3). Higher levels of bioturbation (*ii*4-5), those often linked to the development of “modern” substrate conditions (Bottjer et al. 2000), were not recorded anywhere in either section. The pattern of bioturbation recorded in both is suggestive of Proterozoic-style substrate development (Bottjer et al. 2000). Rare sedimentary fabrics indicative of microbial mat presence (Schieber 1999) were observed; (see previous chapter); however, the characteristic development of Proterozoic-style substrates does not necessarily require the presence of microbial mats (Dornbos and Bottjer 2000; Domke and Dornbos 2010).

4.5.1 *Enrichment factors for V, Cr, Ni, and Zn*: EFs are utilized in numerous paleoenvironmental analyses (Algeo and Maynard 2004; Rimmer 2004; Zhou and Jiang 2009). EFs do not necessarily correlate to redox conditions, but in association with PIs provide a more defined paleoenvironmental context of the Wheeler and Spence Shale settings. EFs were calculated as described in the previous section (see above); enrichments occur when $EF > 1$, and depletions when $EF < 1$. EFs were calculated with respect to (ii)-fabrics (Figs. 4.3-4.10) to highlight the redox-bioturbation relationship, and on a single-axis scale (Fig. 4.11-4.12) to highlight general geochemical conditions.

EFs are more variable than PIs in both the Wheeler and Spence Shales, but some trends are evident. V and Ni are consistently depleted in both shales. Cr and Zn fluctuate from slightly depleted to enriched, with greater and more consistent enrichments of Cr and Zn in the Wheeler Shale, and more consistent depletion of Cr in the Spence Shale. In general, EF values for V, Cr, Ni, and Zn show depletions with respect to average shale concentrations (Wedepohl 1991), suggesting overall oxic bottom water conditions in the Spence Shale, and possible oxic-to-anoxic fluctuations in the Wheeler Shale, which is relatively consistent with interpretations made from the PI data (although see following discussion regarding potential sources for obscuring redox signal in these metals). The Maotianshan Shale samples exhibit EFs consistent with enrichments in all trace metals, suggestive of more reducing conditions compared to the Spence and Wheeler Shales. Comparisons between EF and PI values for the Maotianshan may suggest more dysoxic to potentially oxic conditions compared to the predominantly oxic Spence and Wheeler Shales.

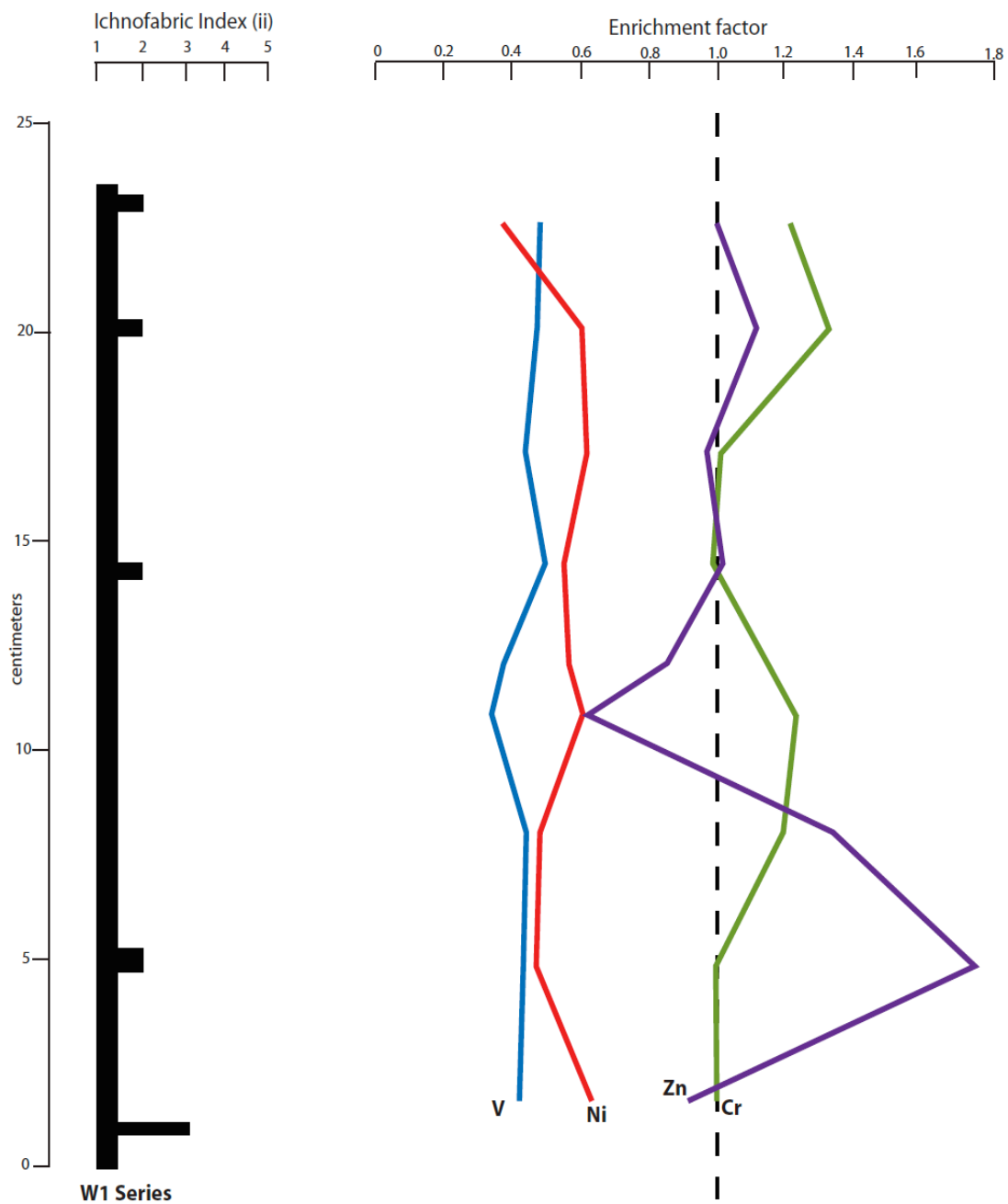


Figure 4.3. Enrichment factors for sample series W1, Wheeler shale.

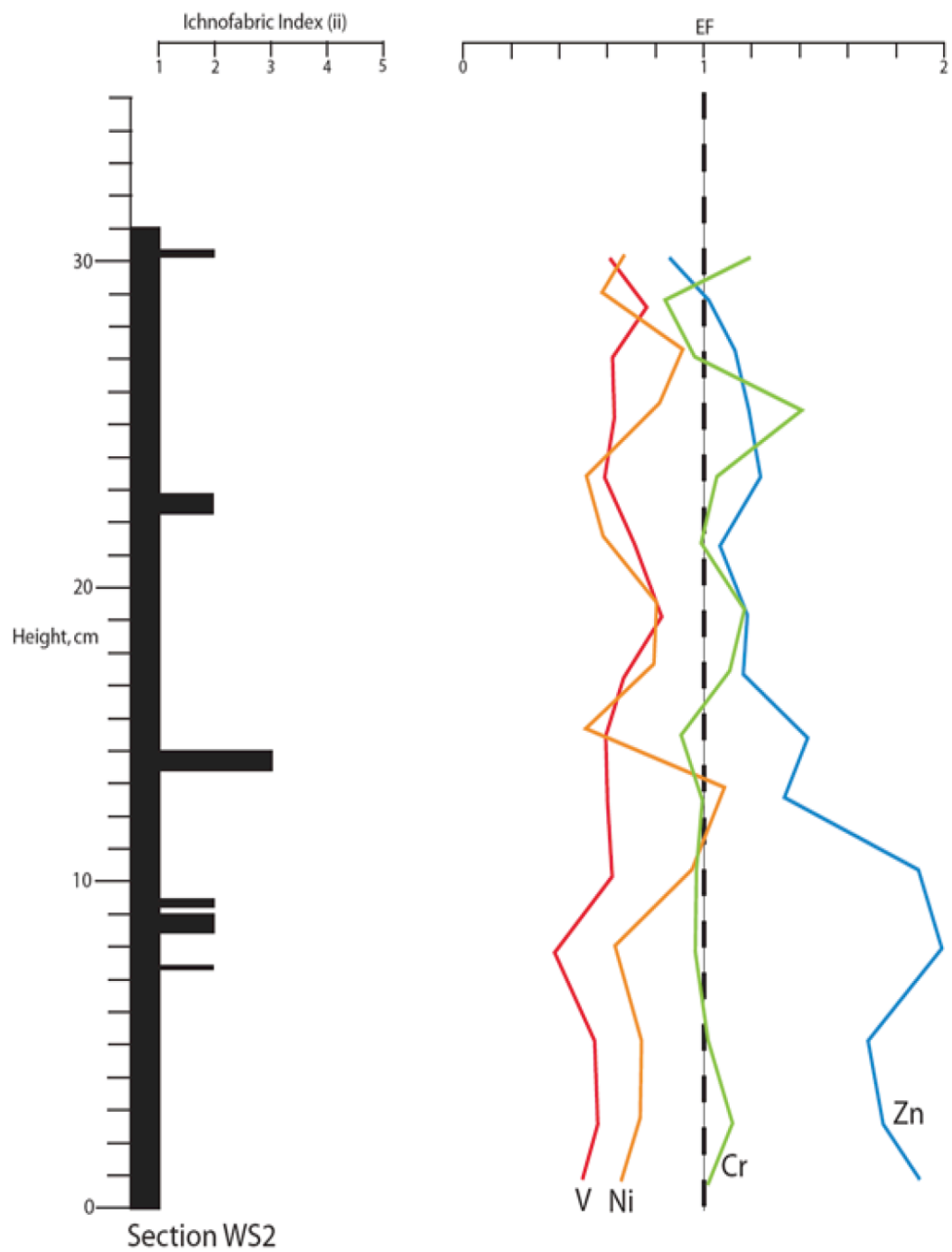


Figure 4.4 Enrichment factors for sample suite W2, Wheeler Shale.

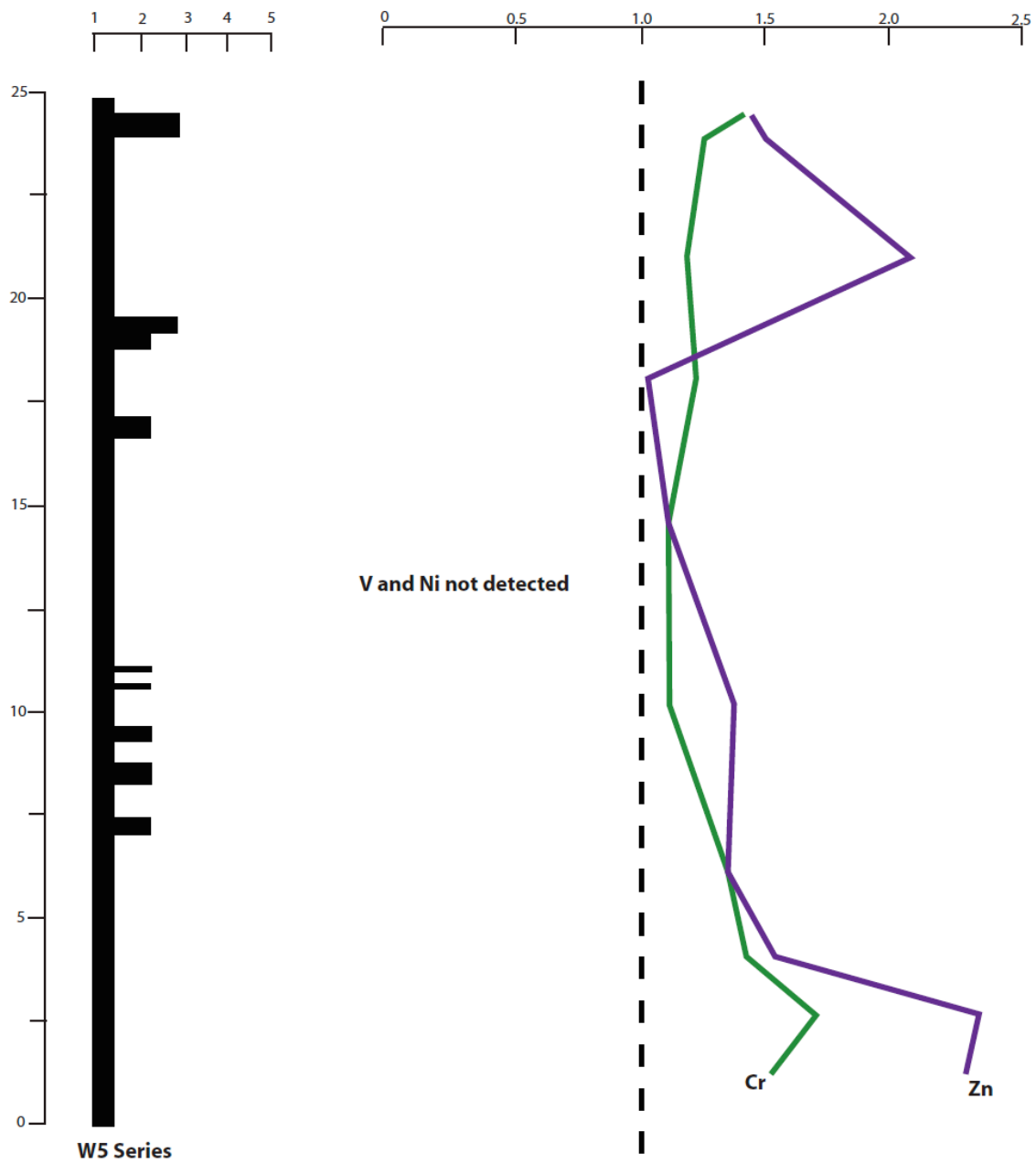


Figure 4.5. Enrichment factors for sample suite W5, Wheeler shale. V and Ni were not detected by the XRF and hence not reported here.

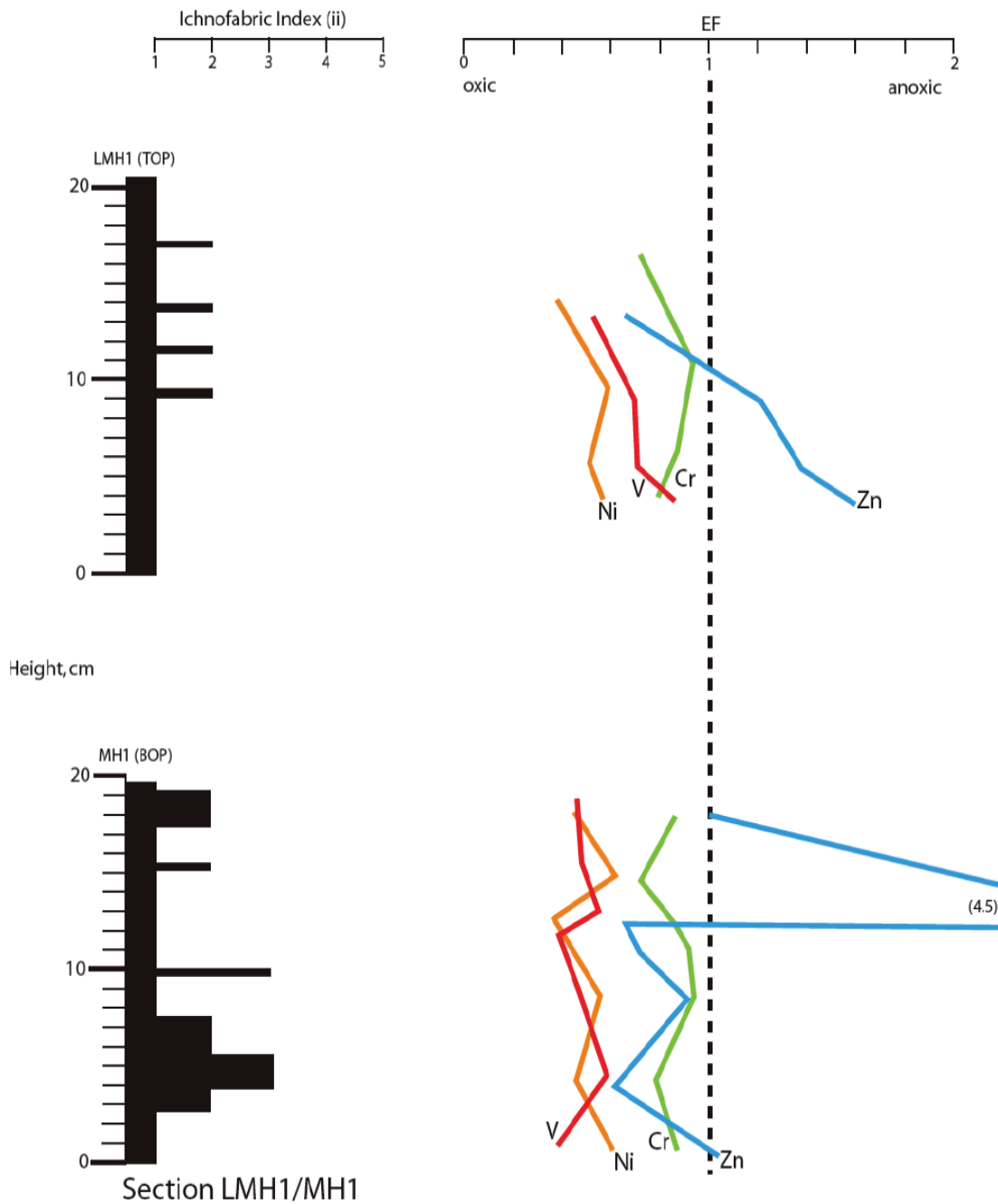


Figure 4.6. Enrichment factors for sample suites LMH1/MH1, Miner's Hollow, Spence Shale.

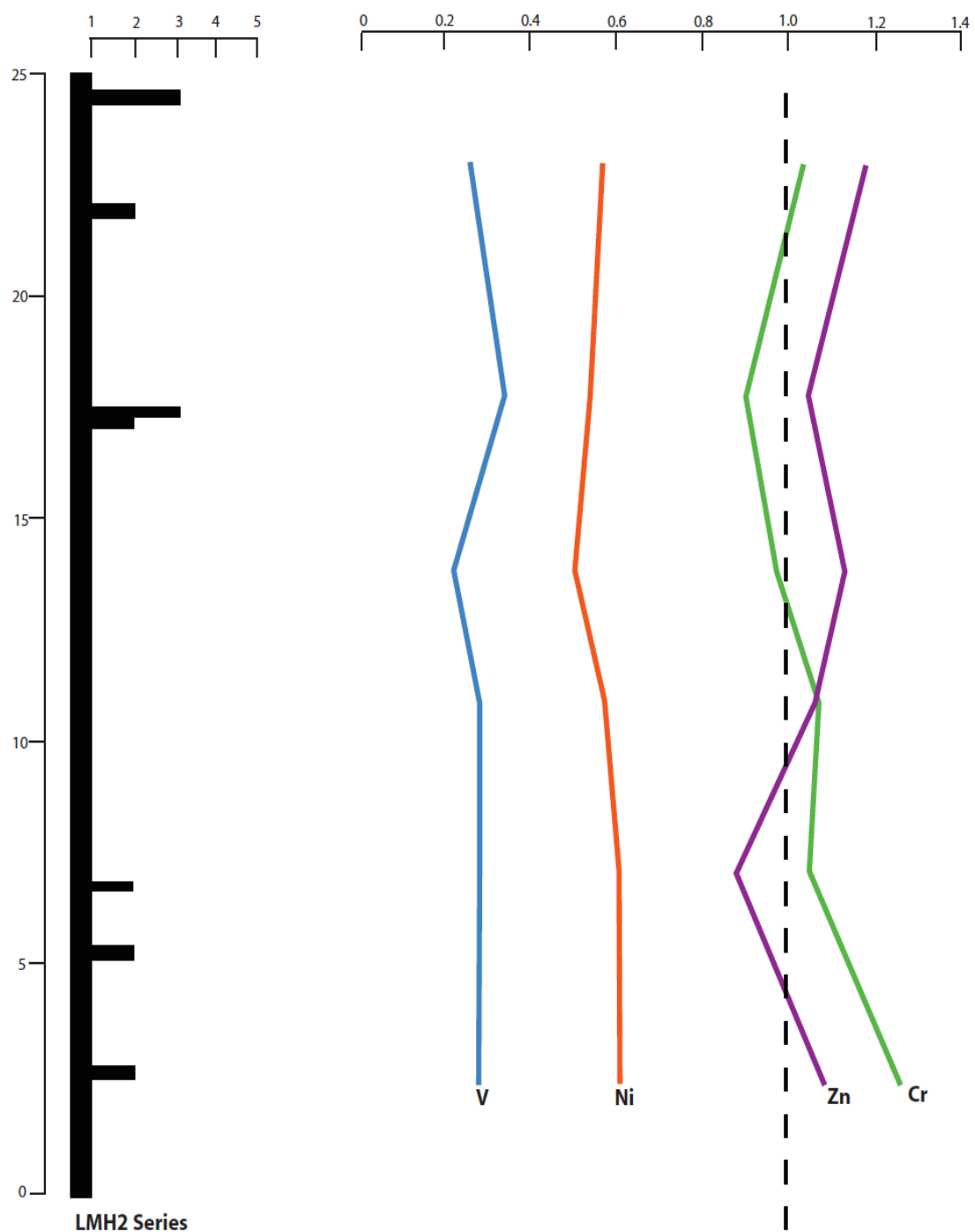


Figure 4.7. Enrichment factors for sample suite LMH2, 5-cm scale, Miner's Hollow, Spence Shale.

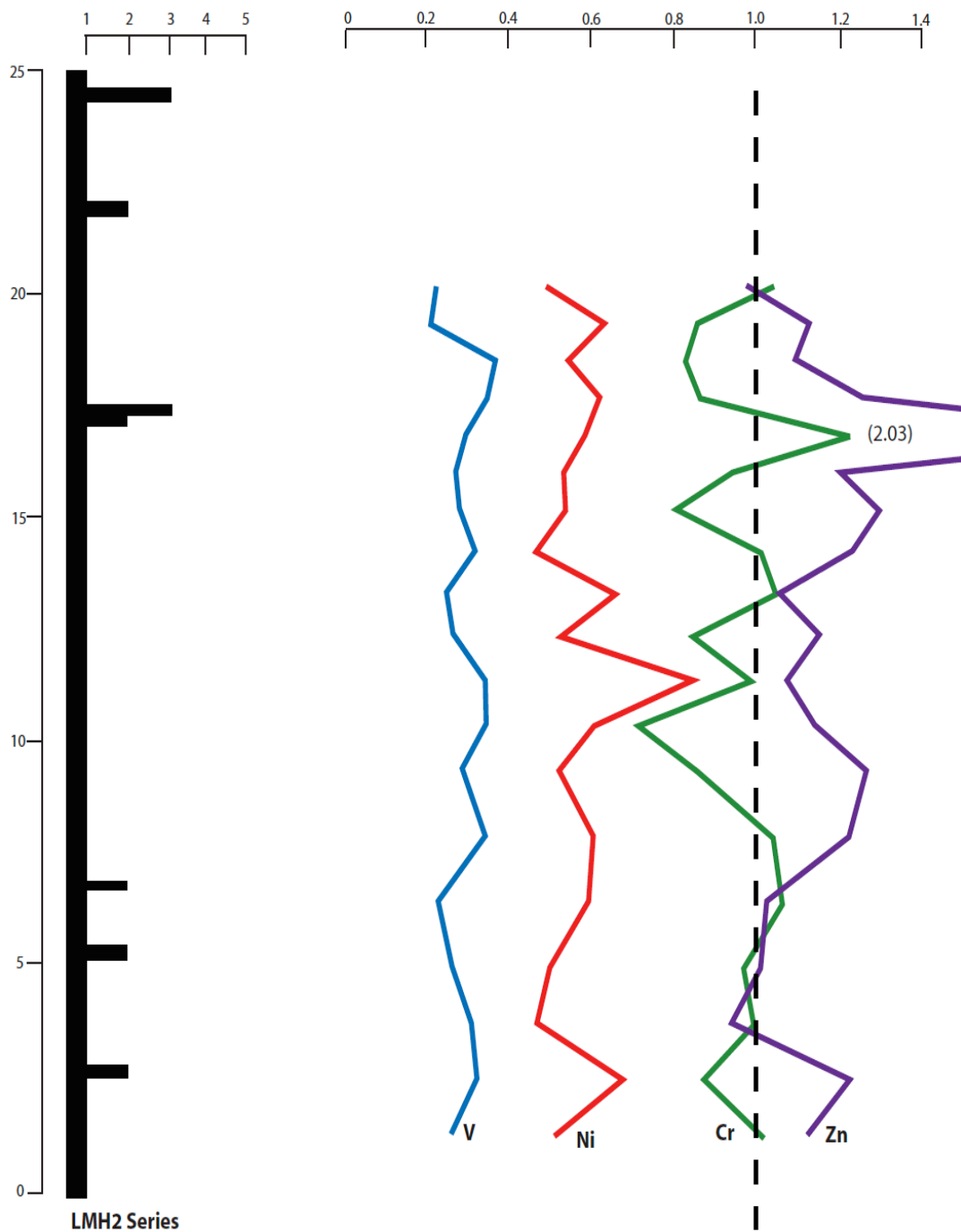


Figure 4.8. Enrichment factors for sample suite LMH2, 1-cm scale, Miner's Hollow, Spence Shale.

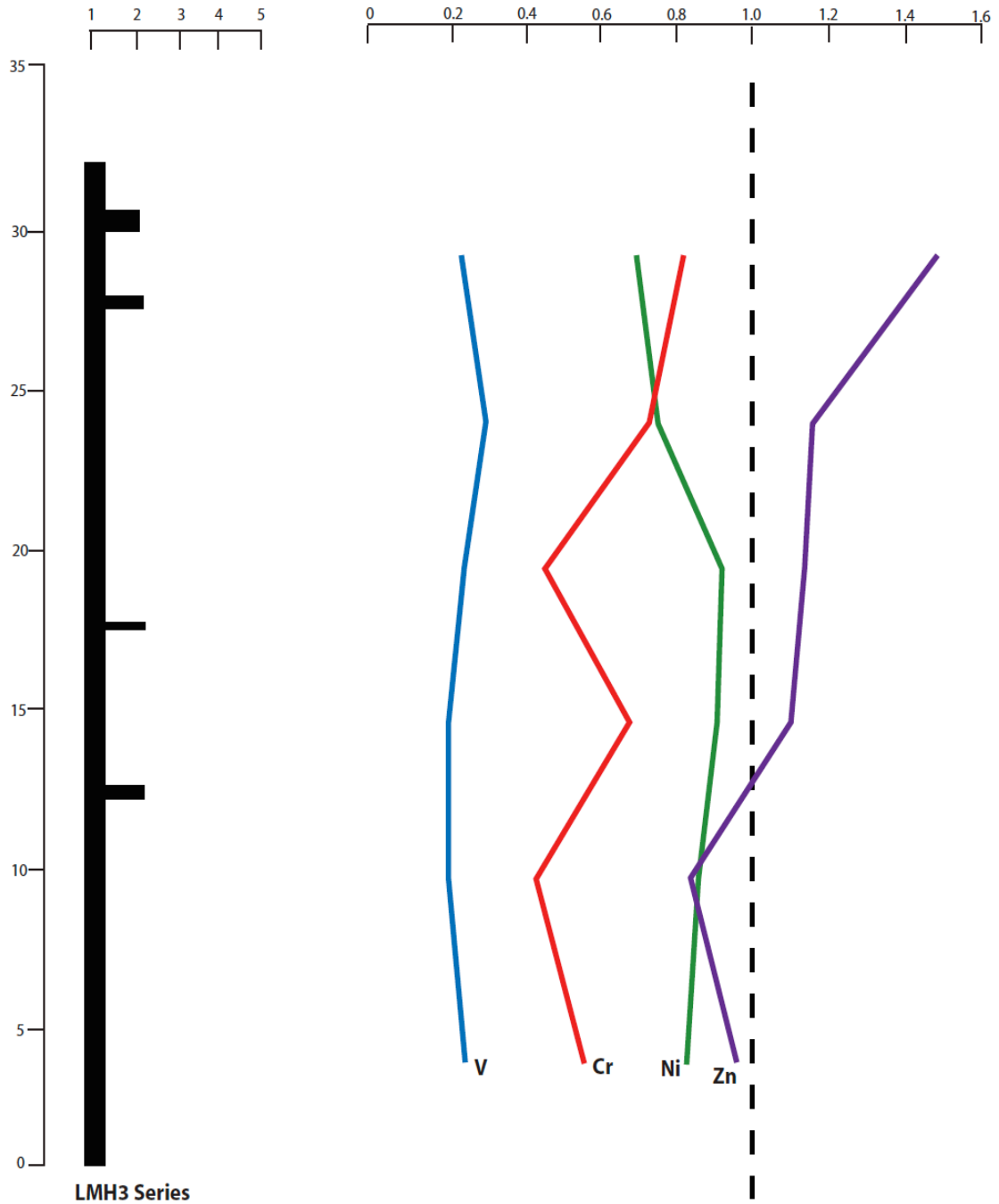


Figure 4.9. Enrichment factors for sample suite LMH3, Miner’s Hollow, Spence Shale.

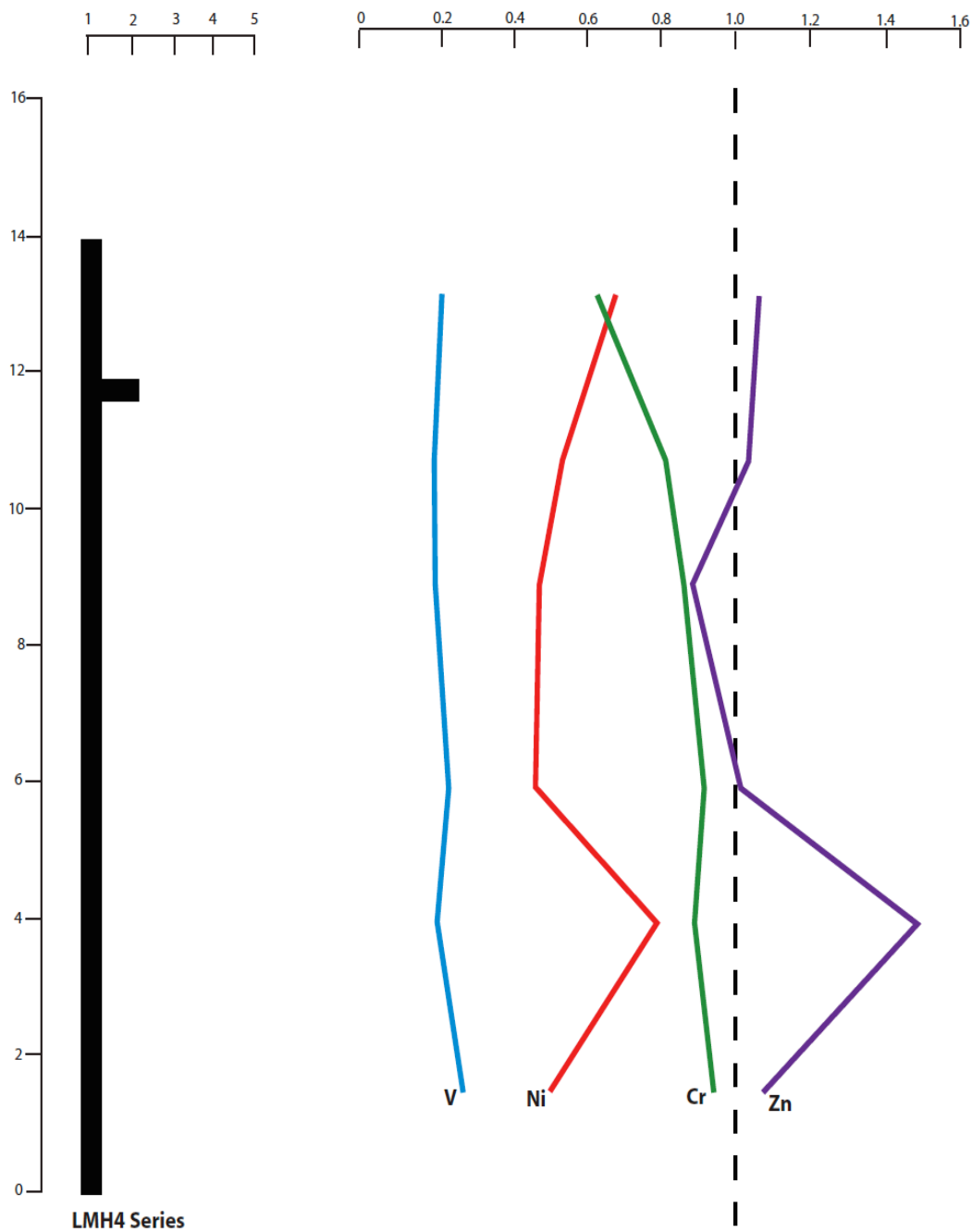


Figure 4.10. Enrichment factors for sample suite LMH4, Miner's Hollow, Spence Shale.

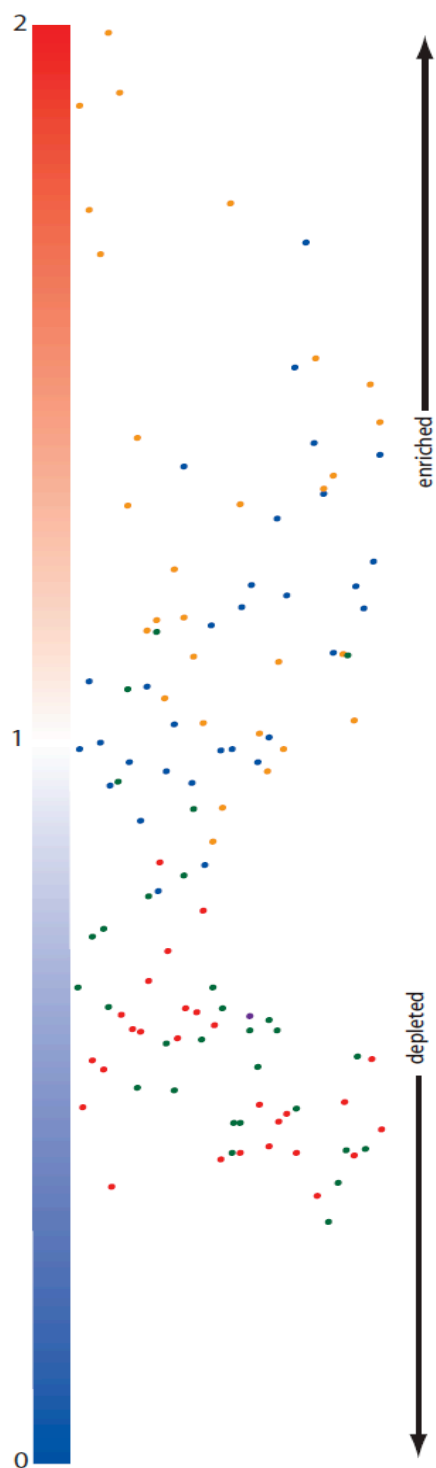


Figure 4.11. Plot of all enrichment factors for Wheeler Shale on single-axis. The overall trend in EF data suggests depletion of redox-sensitive elements with respect to the World Shale Average of Wedepohl (1991). Color corresponds to redox-sensitive element: red is Vanadium; green is Nickel; blue is Chromium; and orange is Zinc.

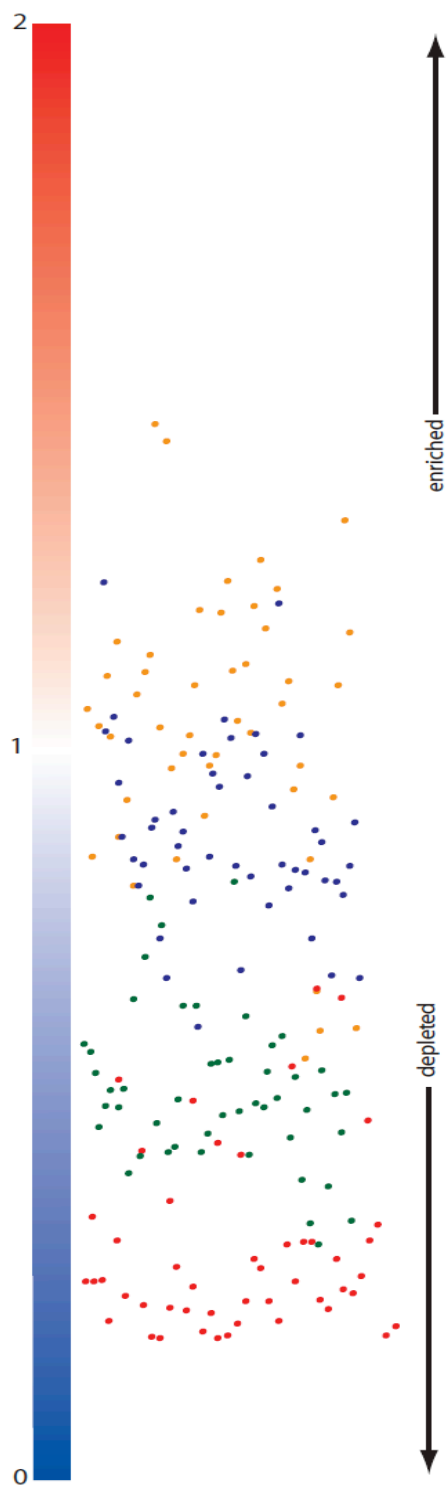


Figure 4.12. Plot of all enrichment factors for Spence Shale on single-axis. The overall trend in EF data suggests depletion of redox-sensitive elements with respect to the World Shale Average of Wedepohl (1991). Color corresponds to redox-sensitive element: red is Vanadium; green is Nickel; blue is Chromium; and orange is Zinc.

4.5.2 *The paleoredox indices V/Cr and V/(V+Ni)*: Paleoredox indices (PI) (Fig. 4.13-4.22) are commonly utilized for geochemistry-based paleoenvironmental analysis of Cambrian shales (Powell 2009; McKirdy et al. 2010) since they provide less ambiguity in paleoenvironmental interpretation compared to enrichment factors (EF). Multiple PIs have been demonstrated as reliable indicators of redox conditions in shales (Jones and Manning 1994; Kimura and Watanabe 2001; Schovsbo 2001; Kimura and Watanabe 2001). The PIs V/Cr and V/(V+Ni) —in addition to U/Th, V/Sc, and Ni/Co— were both utilized by Powell et al. (2003) in his initial paleoredox study of the Burgess Shale, after a review of previous geochemical research demonstrated these PIs to be the most reliable indicators of redox conditions. Schovsbo (2001) also used V/(V+Ni) exclusively in a study of the middle Cambrian Scandinavian Alum Shale. Later studies by Powell (2009) and McKirdy et al. (2011) also make use of V/Cr, but not V/(V+Ni). Powell et al. (2003) suggested that V/Sc and Ni/Co preserved paleoredox conditions in greater detail, and thus is the likely reason why later studies focus upon these PIs. Kimura and Watanabe (2001) also suggest that V/Sc is a more sensitive PI than V/Cr. While this study initially planned on utilizing V/Sc and Ni/Co, Sc and Co were not detected by the XRF. V/Cr and V/(V+Ni) were viable alternatives, and are still considered useful PIs (Powell et al. 2003), demonstrating consistency with the more commonly used V/Sc and Ni/Co (Powell et al. 2003; Powell 2009; McKirdy et al. 2011). For V/Cr, the PI ratio is correlated to redox zones: <2.00 is in the oxic zone, 2.00-4.25 is the dysoxic zone, and >4.25 is the anoxic zone (Jones and Manning 1994). For V/(V+Ni) there is no distinguishing between oxic-

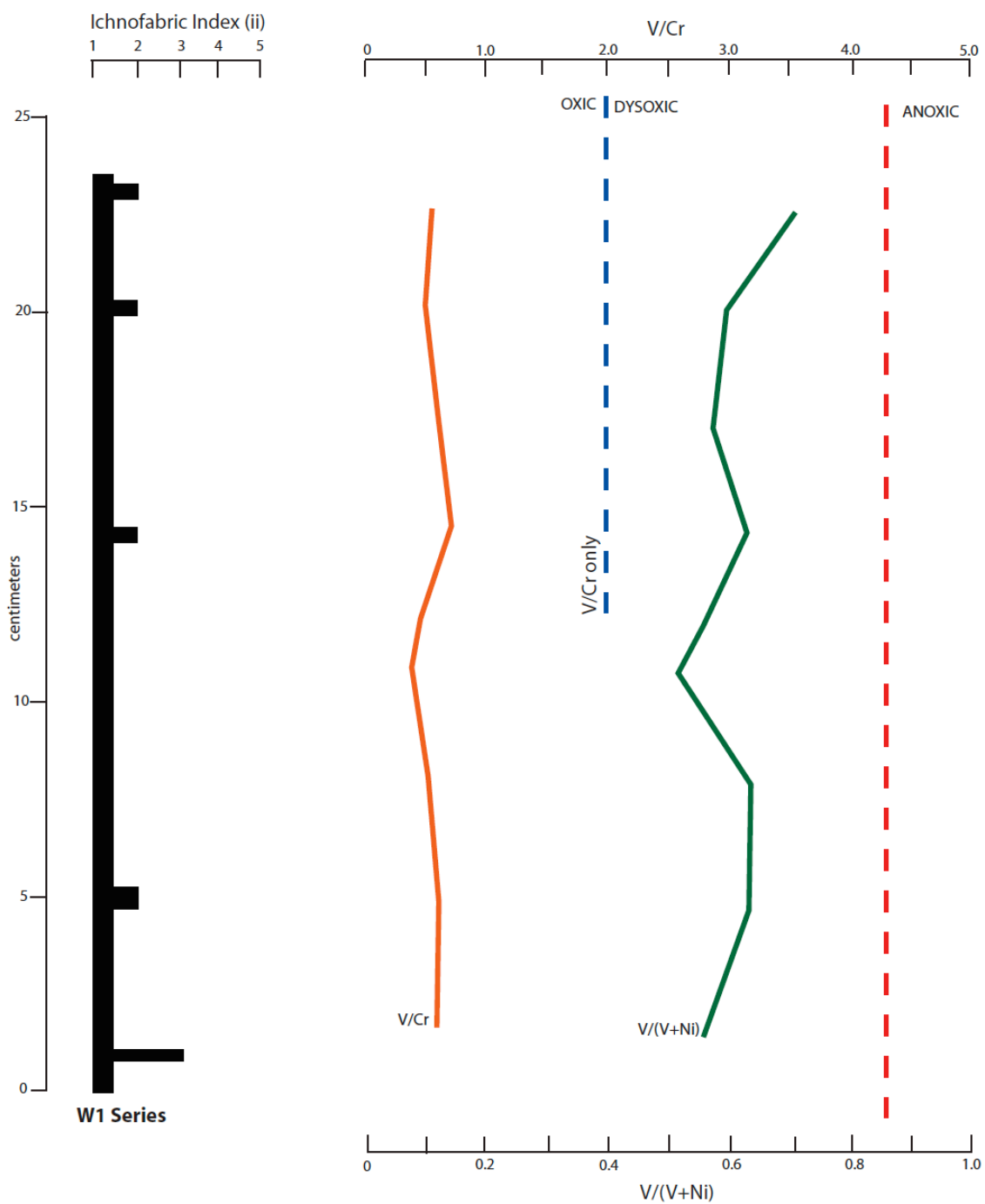


Figure 4.13. Paleoredox indices for sample suit W1, Wheeler Shale.

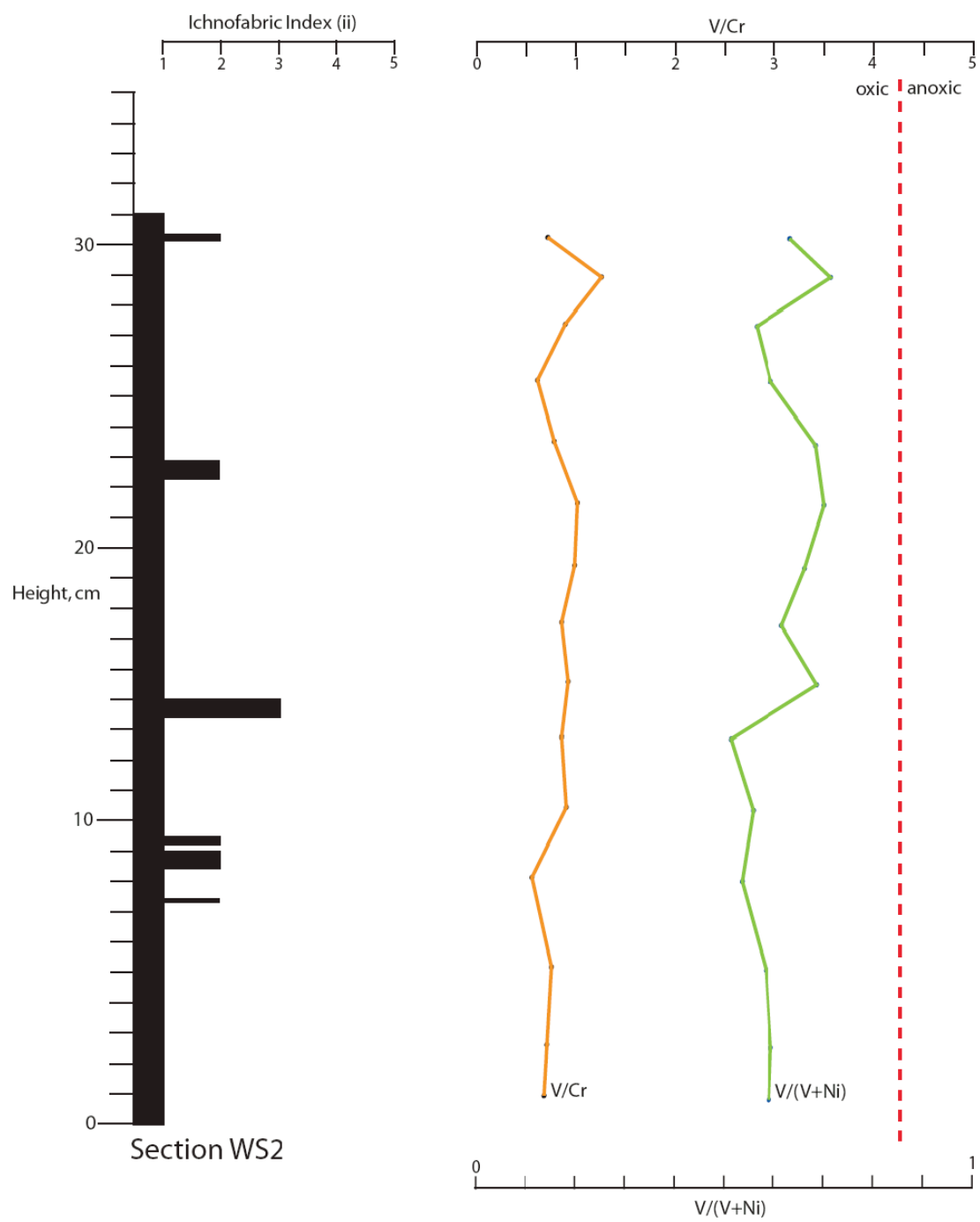


Figure 4.14. Paleoredox indices for sample suite W2, Wheeler Shale.

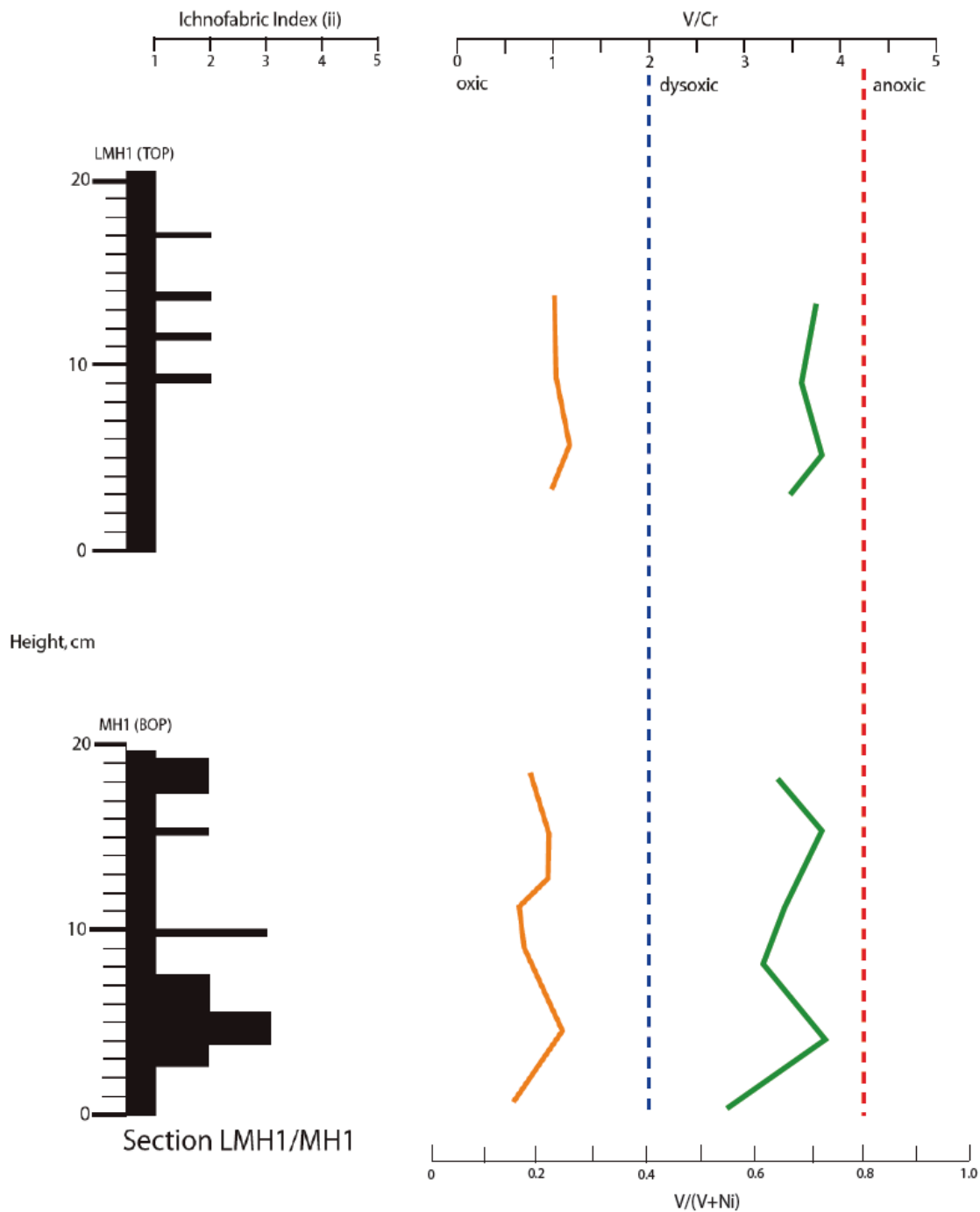


Figure 4.15. Paleoredox indices for sample suite LMH1/MH1, Miner's Hollow, Spence Shale.

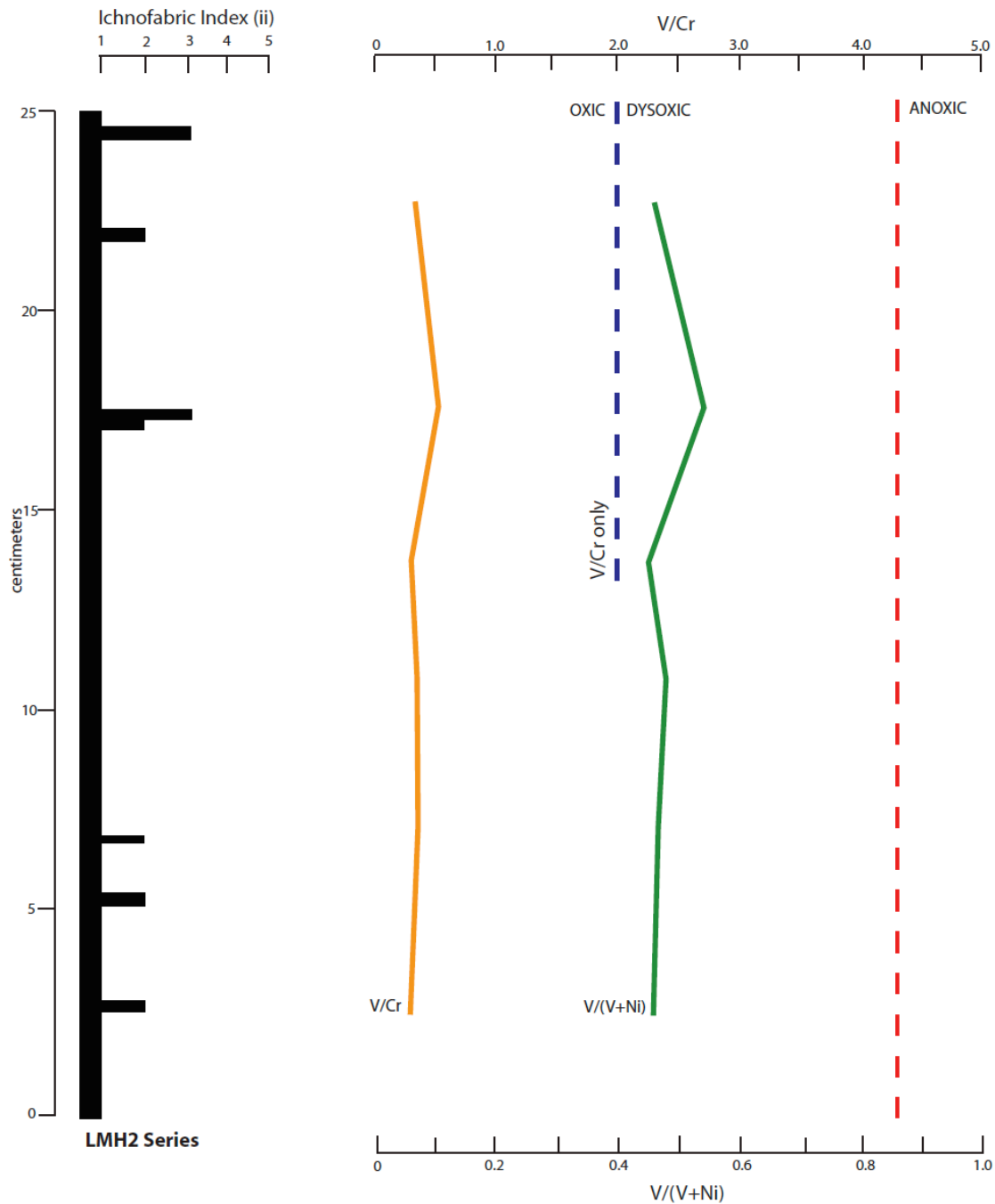


Figure 4.16. Paleoredox indices for sample suite LMH2, 5-cm scale, Miner's Hollow, Spence Shale.

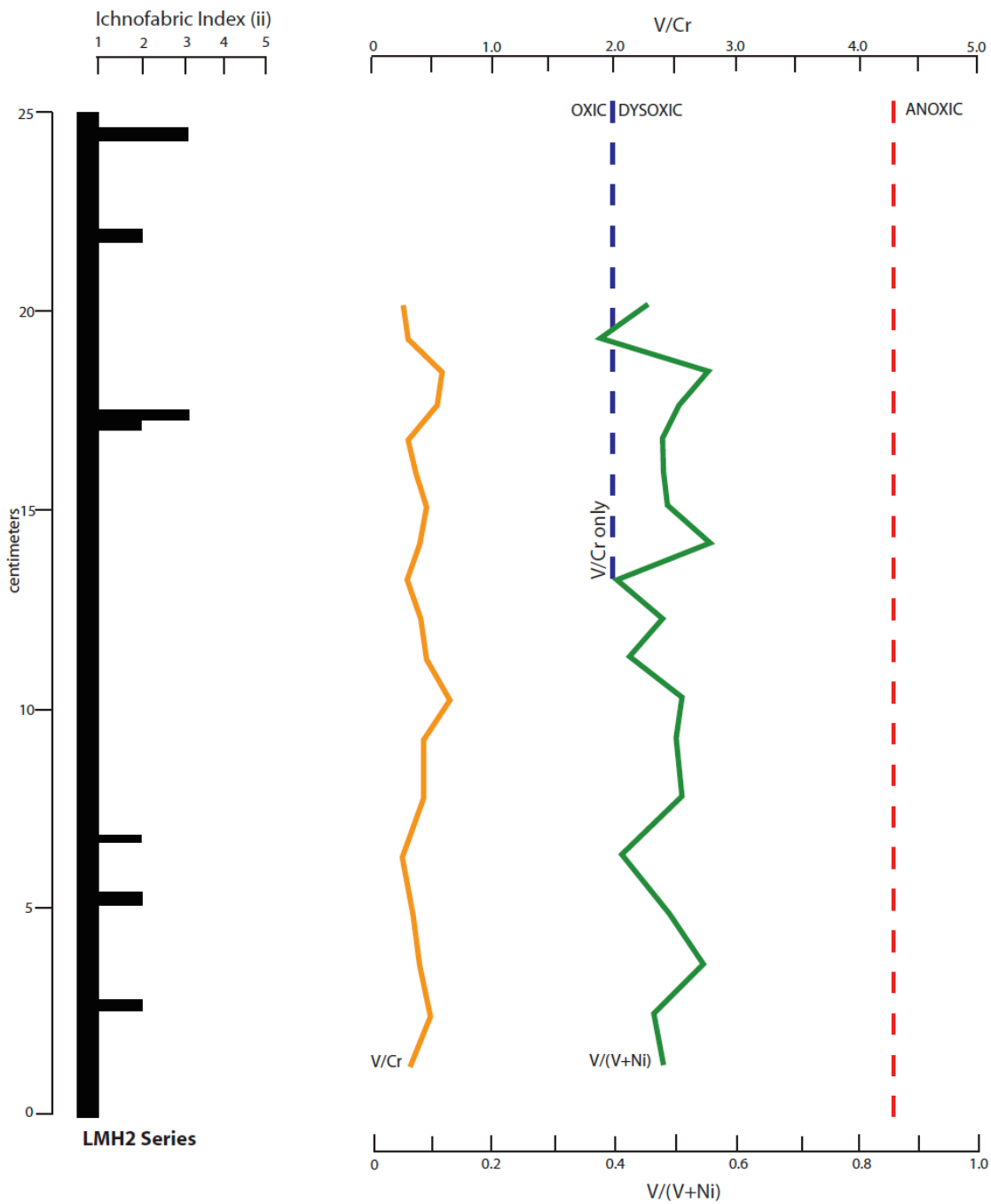


Figure 4.17. Paleoredox indices for sample suite LMH2, 1-cm scale, Miner's Hollow, Spence Shale.

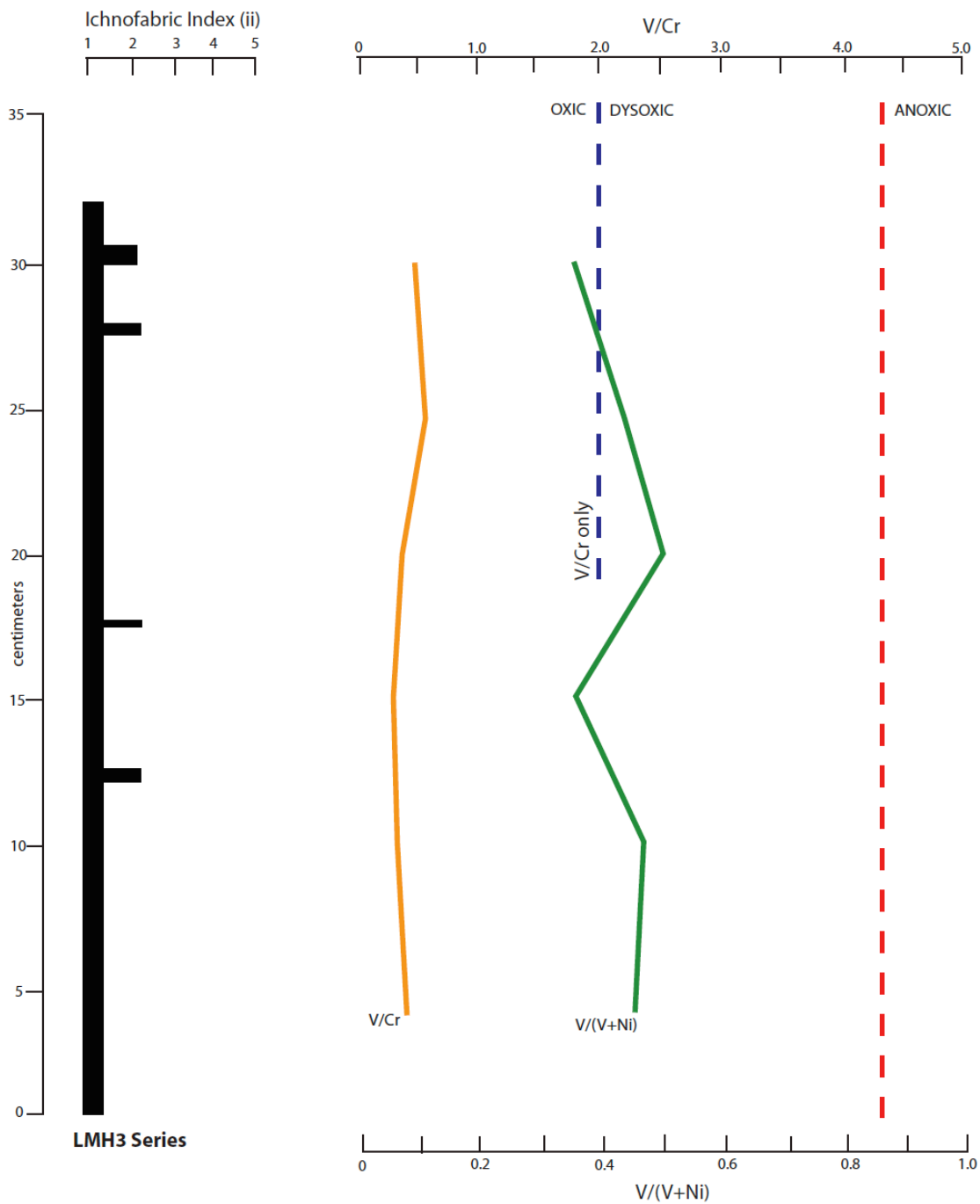


Figure 4.18. Paleoredox indices for sample suite LMH3, Miner's Hollow, Spence Shale.

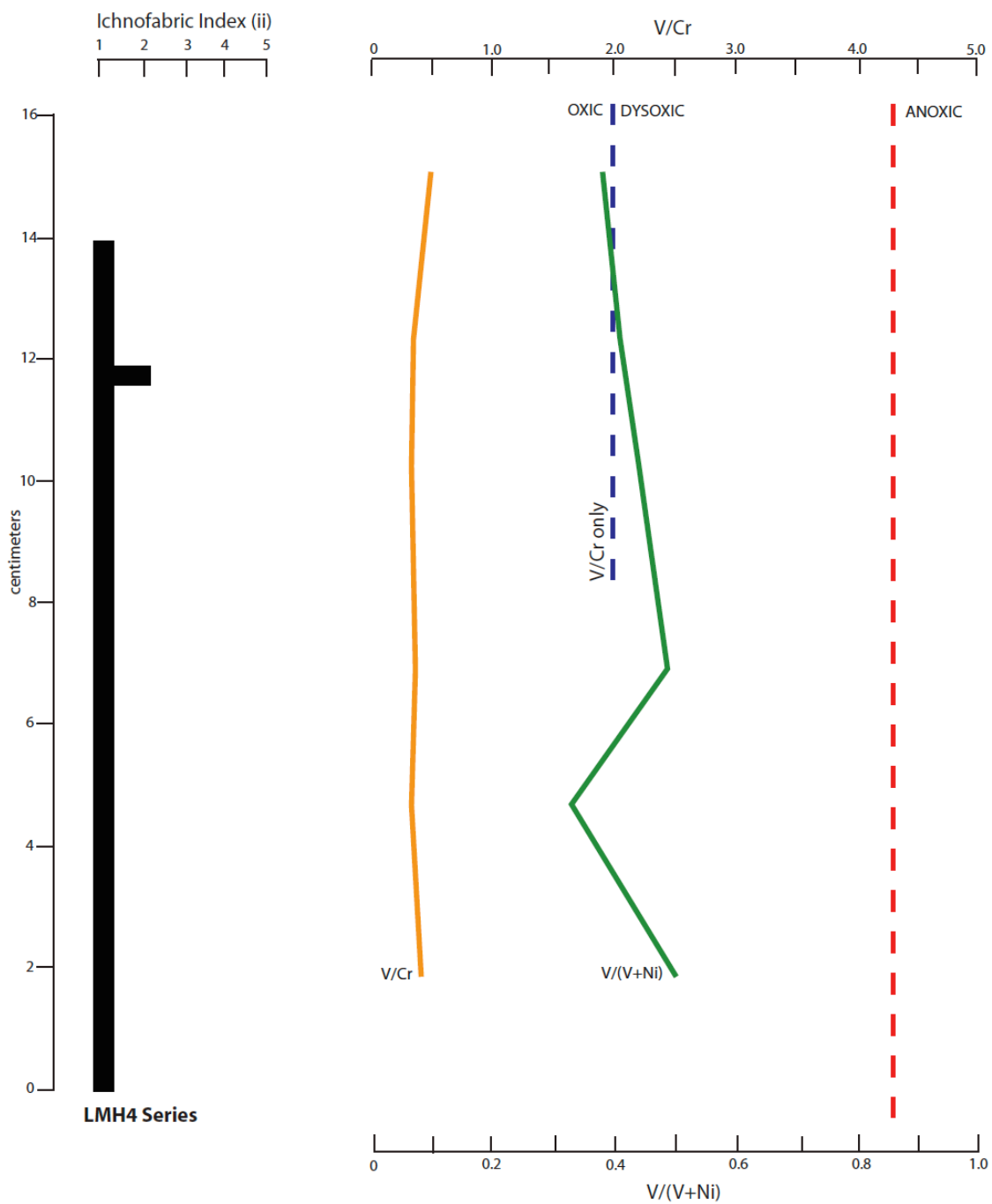


Figure 4.19. Paleoredox indices for sample suite LMH4, Miner's Hollow, Spence Shale.

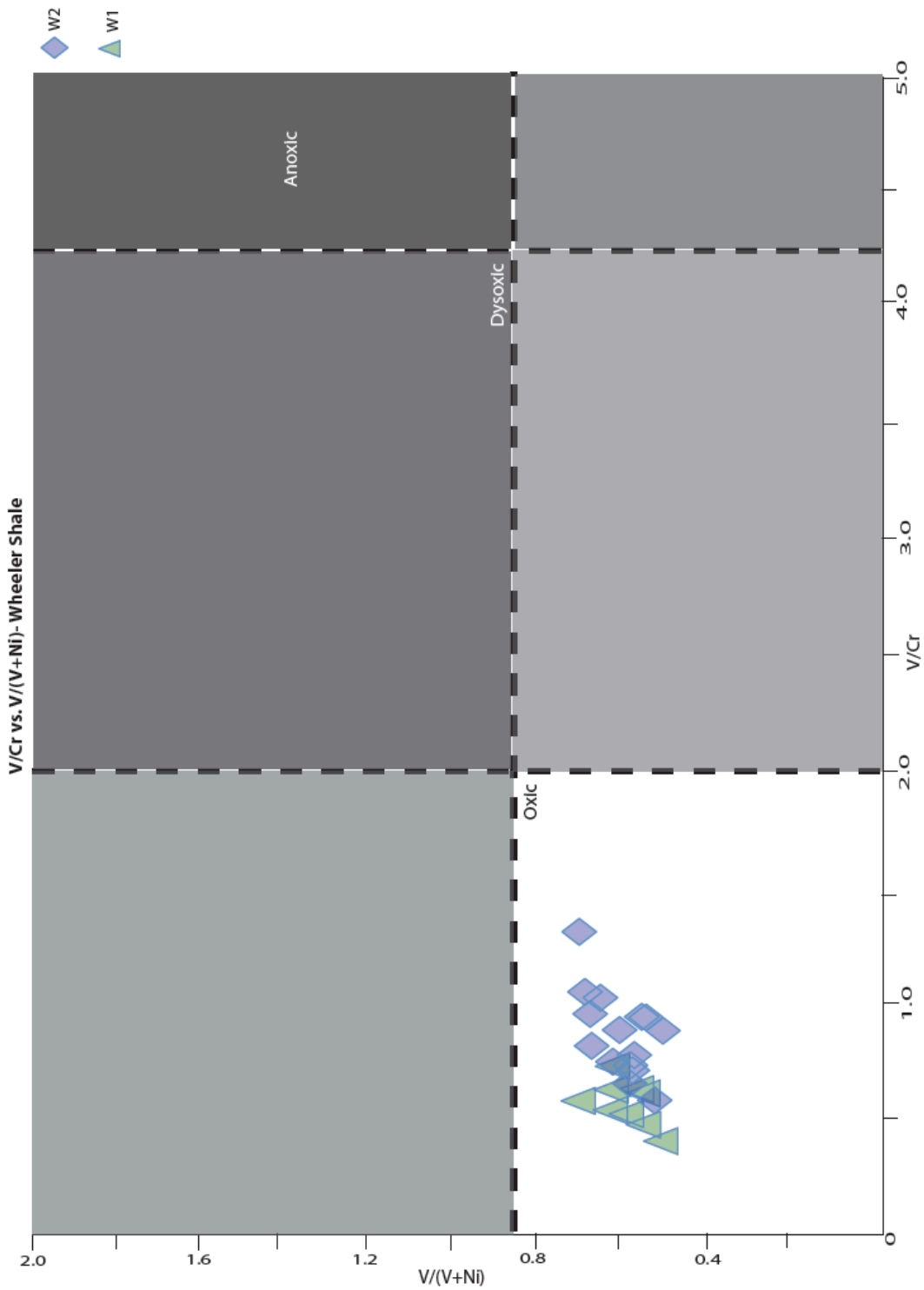


Figure 4.20. Plot of $V/(V+Ni)$ versus V/Cr for the Wheeler Shale. W5 not plotted because V and Ni were not detected.

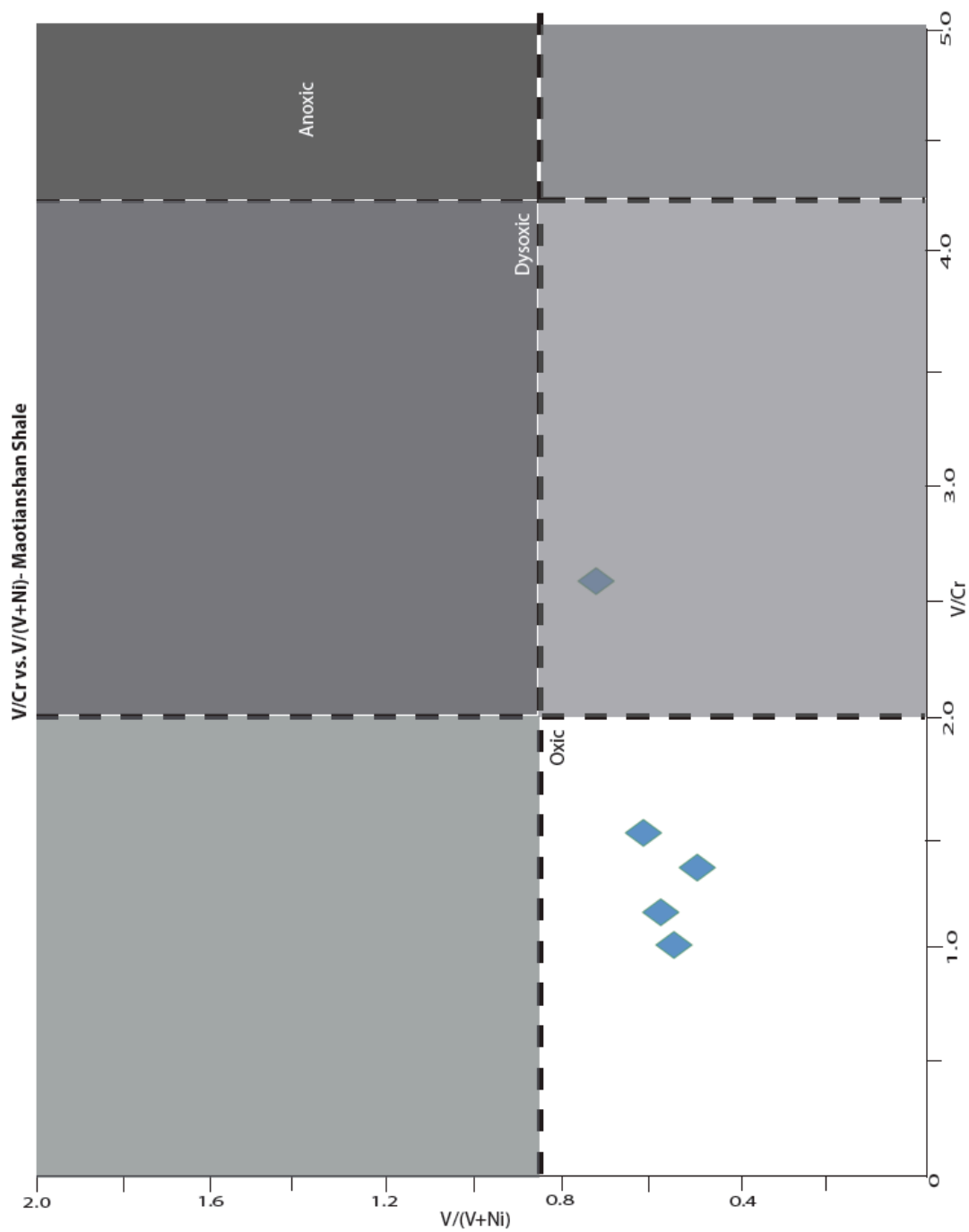


Figure 4.22. Plot of $V/(V+Ni)$ versus V/Cr for samples from the Maotianshan Shale, China.

dysoxic zones, but Schovsbo (2001) suggests that ratios >0.84 correlate to anoxic conditions.

V/Cr and V/(V+Ni) ratios are plotted relative to ichnofabric indices in Figs. 4.13-4.20 to highlight relationship between bioturbation and redox conditions, and PIs are plotted versus each other in Fig. 4.21-4.23 to highlight small-scale variations between redox zones. Overall redox conditions in both Wheeler and Spence Shales are dominantly oxic. Significantly, with the exception of a single sample (M4A, V/C r= 2.6) V/Cr and V/(V+Ni) ratios rarely approach the oxic-dysoxic boundary ($0.19 < V/Cr < 1.50$, and $0.34 < V/(V+Ni) < 0.81$), suggesting possible mildly dysoxic conditions in portions of the Wheeler and Maotianshan Shales, and in the Spence Shale at the Oneida Narrows.

General comparisons between PIs and (ii)-fabrics demonstrate that bioturbation was lacking in Spence and Wheeler Shale paleoenvironments despite oxygenation of the bottom water. The lack of Phanerozoic-style correlation between redox conditions and bioturbation suggests that Proterozoic-style substrates were at least present, if not abundant, in both shales. Direct correlations between mm-scale changes in (ii)-fabrics and PIs are more difficult to determine, due in large part to the scaling differences between the ichnofabric and geochemical analyses. This is evident when comparing the 5-cm- and 1-cm-scale analysis for LMH2. At the 5-cm-scale there appears to be correlation between moderately (ii2-3) bioturbated beds at 18cm and an excursion in both the V/Cr and V/(V+Ni) values (Fig. 4.17), suggesting a relationship between bioturbation and redox variability. At the 1-cm-scale, however (Fig. 4.18), it becomes

apparent than the redox excursion occurs ~1cm above the moderately bioturbated beds. In addition multiple other excursions occur through the column, not observed at the coarser scale, which do not correspond to any observed variations in bioturbation. Thus, caution must be taken not to infer too much from the apparent discrete relationships between redox and bioturbation.

4.6 Discussion

The paleoredox results presented here, and their comparison to ichnofabric data, are strongly suggestive of the independence of redox and substrate conditions, quite unlike the co-dependent relationship observed in modern marine environments. Modern substrate conditions owe a great deal to the presence of dissolved oxygen: when dissolved oxygen is abundant infaunal activity is common, traces and trackways are diverse, and bioturbation is extensive; and when dissolved oxygen is scarce infaunal activity is low, trace and trackways are of low diversity, and bioturbation is minimal or absent (Ekdale and Mason 1998). This is not the type of relationship we see with the Spence and Wheeler Shales: bioturbation levels remain low even as paleoredox conditions exhibit some fluctuations through time, and changes in burrowing intensity overall are not strongly correlated to changes in paleoredox conditions. This suggests that paleoredox conditions are not a controlling factor, or have minimal influence, upon bioturbation levels and subsequent substrate conditions in the Spence and Wheeler Shales. Rather, with our knowledge of Cambrian substrates already established, the comparative analysis here suggests that Proterozoic-style substrates were a controlling

factor on substrates, suppressing bioturbation even when paleoredox conditions reached well-oxygenated levels. This confirms the hypothesis that the Spence and Wheeler Shale substrates and corresponding benthic faunas were controlled by Proterozoic-style substrates.

4.6.1 Interpreting the redox signal from enrichment factors: EFs gauge the relative enrichment or depletion of a given trace metal with respect to a hypothetical average shale, and is not a direct correlation to estimates of redox conditions. Redox conditions can be determined in a relativistic manner, however, by comparisons between trace metals and an understanding of how each metal is cycled through marine seawater.

Of the four trace metals examined here, V has the most “pure” redox signal, as it does not have a strong detrital source (Tribovillard et al. 2006) and has minimal involvement in biogeochemical cycles in surficial waters (Calvert and Pedersen 1993). In general V, along with Mo and U, is considered a redox proxy for deposition under dysoxic or anoxic conditions (Calvert and Pedersen 1993; Tribovillard et al. 2006; Piper and Calvert 2009). The lack of V enrichment in the Spence and Wheeler Shales suggest generally oxic bottom water conditions, while the slight depletion to slight enrichment of V in the Maotianshan is suggestive of more reducing conditions.

Cr also accumulates under reducing conditions, mimicking the behavior of V, but it has much stronger detrital source (Tribovillard et al. 2006) and shows greater influence in biogeochemical cycling (Calvert and Pedersen 1993). Tribovillard et al.

(2006) suggests that the influence of the detrital fraction can be roughly estimated based upon the correlation between the trace metal and Al (which is dominantly of detrital origin in normal sediments), assuming that trace metal abundance is comparable to average abundances. A statistical calculation of r shows strong correlation between Cr and Al in the WS1, WS2, and WS5 ($r = 0.71, 0.79, \text{ and } 0.80$, respectively), which contrasts sharply with low correlations in the Spence ($r = 0.12$ LMH2, $r = 0.48$ LMH3, $r = -0.39$ LMH4) and suggests a strong detrital influence in Cr deposition in the Wheeler Shale. Cr abundance is well below average (mean = 62ppm versus average = 90ppm); however so too are Al abundances in the Wheeler (mean = 54033ppm versus average = 88900ppm), suggesting that overall terrestrial input in the Wheeler may have lagged behind average marine sediments (for comparison, Al mean = 107610ppm in the Spence). Thus, the EF values of Cr are more limited in their application to redox conditions, although the general lack of significant enrichment with respect to average would suggest at the very least that depositional conditions were not strongly reducing.

Ni is more complex than either V or Cr, as it is primarily delivered to sediments by adsorption with organic matter (OM), and then rereleased into pore waters following OM decay (Tribovillard et al. 2006). Rerelease of Ni can occur even under moderate reducing conditions, but Ni may be trapped in sediments as part of the solid solution of pyrite under strongly reducing conditions in the presence of free sulfides (Morse and Luther 1999). Ni is generally enriched in sediments in modern anoxic basins (Calvert and Pedersen 1993). If OM settling is not abundant in the depositional setting, than Ni will

not be significantly enriched in sediments regardless of redox conditions (Tribovillard et al. 2006). Depletions of Ni in the Spence and Wheeler Shales either suggest a lack of strongly reducing conditions or a lack of OM flux in the depositional environment, the former interpretation being consistent with V accumulations. Conversely, the enrichment of Ni in the Maotianshan Shale may speak to strongly reducing conditions, which contrasts with the V redox signal. Tribovillard et al. (2006) suggests that Ni should be used as a proxy for OM flux rather than redox conditions. Thus a more conservative interpretation of Ni enrichment would suggest OM flux was rather low for the Spence and Wheeler Shales, but relatively high for the Maotianshan Shale.

Zn displays the most complex enrichment pattern in the Spence, Wheeler, and Maotianshan Shales. Generally slightly to strongly enriched in the Spence and Wheeler Shales, and slightly depleted in the Maotianshan, Zn is another metal that is delivered to sediments largely through complexation with OM, and released to pore waters upon OM decay (Tribovillard et al. 2006). Under sulfate-reducing conditions it may form insoluble sulfides (Tribovillard et al. 2006), so its enrichment is in stark contrast to depleted V in the Spence and Wheeler Shales. Modern observations of well-oxygenated basins where the redox boundary is located near the sediment surface show accumulations of Zn in the sediment as a sulfide, despite the presence of oxic bottom waters (Calvert and Pedersen 1993). Thus, the enrichments of Zn in the Spence and Wheeler Shales may suggest that the oxic-anoxic boundary is located near or at the sediment-water interface, allowing for the diffusion and precipitation of Zn into relatively anoxic sediments underlying an oxic water column.

Ultimately, the multiple potential pathways toward trace metal enrichment highlight the difficulties in interpretation of trace metal accumulations in marine sediments. Overall, V is likely to offer the strongest support of redox conditions in the three shales examined here (Tribovillard et al. 2006), and combinations of trace metal EFs offer informative conclusions regarding not only paleoredox conditions but also OM accumulation. Comparisons between EFs and paleoredox indices, which are calibrated to give more reliable estimates of redox conditions, offer insight into the overall paleoenvironment conditions of the Spence, Wheeler, and Maotianshan Shales.

4.6.2 Considering scale in paleoredox analysis: The 1-cm- and 5-cm-scales for geochemical analysis presented here represents sampling on a finer scale than any those conducted on comparable Cambrian Shales. For example, McKirdy et al. (2011) collected 24 samples of the Emu Bay Shale over a 7.10m, with a minimum distance of 15cm between sampling intervals and an average of 29.6cm. Powell et al. (2003) do not give specific information regarding sampling intervals, but an estimate based upon review of their methodology suggests sampling must have occurred on the decimeter-to-meter scale. In addition to intensity, it is unclear whether the analyzed material are aggregates of continuously sampled strata—generating a decimeter-to-meter-scale-averaged geochemical signal representing the entire stratigraphic column-- or whether they are a discrete specimens collected on the decimeter-to-meter scale—generating a mm-to-cm-scale-average geochemical signal, but omitting larger portions of the stratigraphic column. McKirdy et al. (2011) obtained ~5g of “representative portions”

from larger ~2kg specimens collected from the Emu Bay Shale, which implies discrete sampling.

In contrast to geochemical analysis, ichnological (fabric and faunal) studies of Cambrian shales are carried out at the bedding scale or finer, resulting in sampling intensities at the mm-to-cm scale (Gaines and Droser 2003; Dornbos et al. 2005; Garson et al. 2008; Domke and Dornbos 2010). In their criticism of geochemical redox studies, Gaines and Droser (2010) make note of this discrepancy and suggest that the coarse scale of geochemical study will unavoidably obscure the paleoredox signal generated by multiple smaller scale adjacent beds. This obscured signal leads to a generalization of redox conditions and ignores bed-to-bed variations in oxygenation, which is critical for proper interpretation of paleoenvironment, paleoecology, and taphonomy.

If Gaines and Droser (2010) are correct, one would expect to find increasing variability in the geochemical signal for a given stratigraphic section as the sampling scale becomes increasingly small, most significantly transitions between redox conditions. For example, shales exhibiting a consistent oxic signature at the decimeter-to-meter scale may be expected to exhibit oxic-to-anoxic fluctuations at the bedding (cm) scale. Further, this variability may be expected to correspond to significant ichnological, environmental, or taphonomic conditions, i.e. changes in bioturbation intensity or beds containing exceptionally preserved fossil assemblages.

The geochemical analysis presented here resulted in a cm-scale-averaged geochemical signal for the sampled sections for best comparison to ichnofabric data.

However, the Spence Shale exposure at Miner's Hollow was also preferentially sampled at the meter-scale, with specimens collected corresponding to shale units closest to the top and bottom of parasequences identified by Liddell et al. (1997). Thus, it is possible to compare the discretely sampled meter-scale geochemical signal to that of the continuously sampled 1- and 5-cm-scale signal in order to evaluate the impact that scaling has upon paleoredox interpretations.

Liddell et al. (1997) described seven parasequences in the Spence Shale at Miner's Hollow (MC1-MC7). These parasequences were identified in the field by stratigraphic relationships as well as a random count of polymeroid and agnostid trilobite abundances (Liddell et al. 1997). Specimens were then collected at outcrops identified as the top and bottom of parasequences MC3 through MC7. Shale beds from MC1 and MC2 were not well exposed and thus not sampled. The bottom of parasequence MC5 and top of parasequence MC7 were likewise not sampled. In total, eight discrete sections of strata were sampled from the Miner's Hollow locality, which span ~37m of vertical distance from the base of MC3 to the base of MC7. The discrete meter-scale geochemical analysis of V/Cr and V/(V+Ni) was then compared to the continuous 1- and 5-cm-scale analyses of section LMH2, which corresponds to the base of MC4 (Fig. 4.24). Variations in PI values are rather indistinguishable between the 1- and 5-cm-scales ($0.30 < V/Cr < 0.67$ at 1-cm versus $0.32 < V/Cr < 0.54$ at 5-cm; and $0.38 < V/(V+Ni) < 0.56$ at 1-cm versus $0.46 < V/(V+Ni) < 0.56$ at 5-cm), and there is no significant difference in terms of redox signal variability between the meter- and cm-

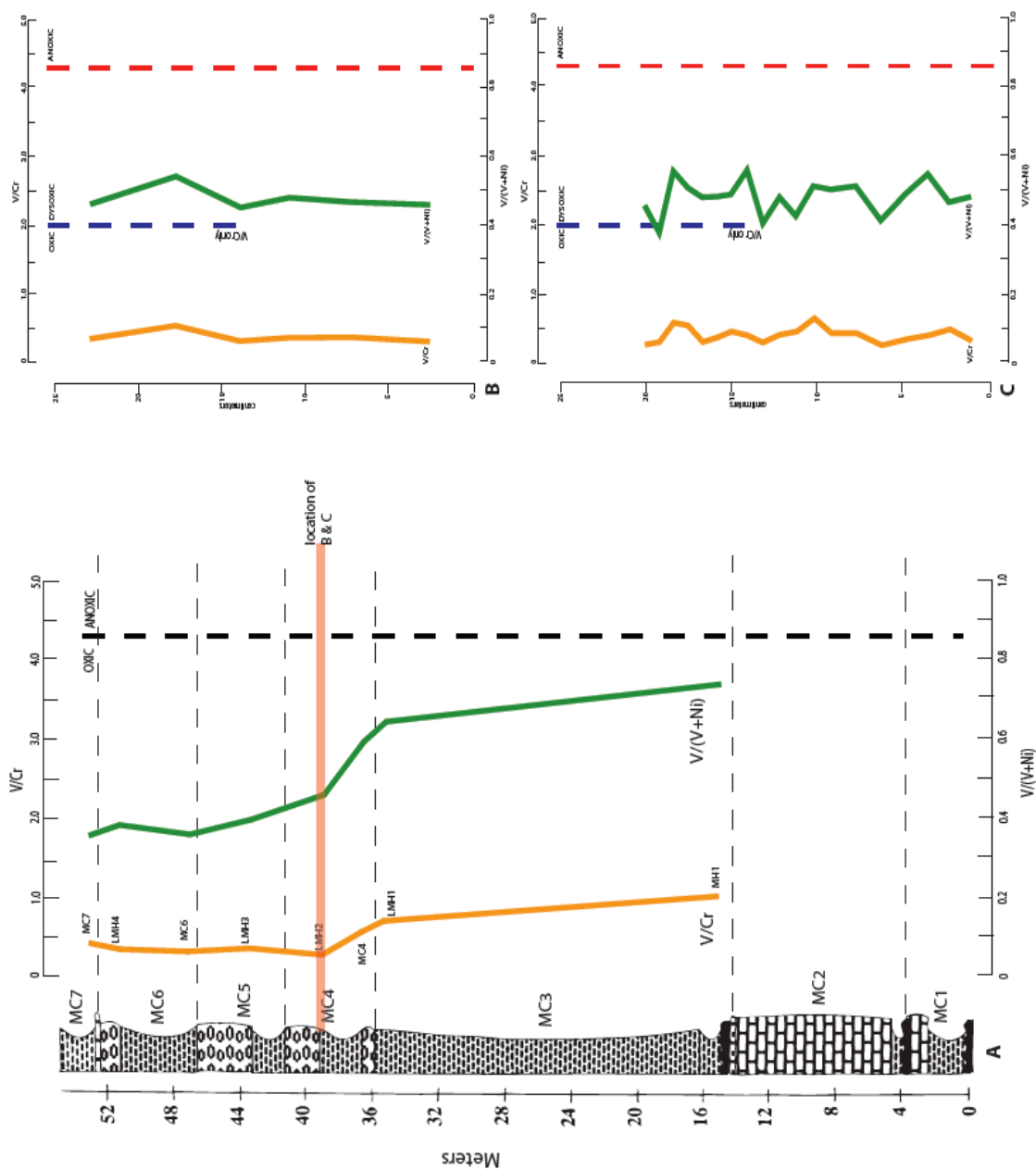


Figure 4.23. Geochemical analysis for Miner's Hollow at the (a) meter, (b) 5-cm, and (c) 1-cm scale. Stratigraphic column modified from Liddell et al. (1997).

scales. The geochemical signal is dominantly oxic at every scale, and most notably there are no measured transitions across redox boundaries. Comparisons between the meter-scale analysis and 5-cm-scale analysis for MH1, LMH1, LMH4, and LMH4 also demonstrate consistency in geochemical signal and a lack of measured transitions across redox boundaries. Regardless of scale, geochemical analysis indicates that the Spence Shale was deposited under oxic conditions.

Granted, this will likely fail to satisfy some critics of the geochemical approach. While ~2 m worth of material was sampled and analyzed on the cm-to-mm scale for this study, a large portion of Spence Shale (and the Wheeler) was not given more than a cursory field examination. Thus, the potential to measure geochemical transitions across redox boundaries in the remaining section still exists. From a practical standpoint sampling at the mm-to-cm scale with the intent of performing a geochemical analysis is unrealistic due to both time and cost. In cases where direct bed-by-bed measurements would be informative, i.e. beds with exceptional fossil preservation, a methodology similar to that utilized here may be most effective. Sampling intensities should be highest surrounding beds of interest whereas less significant layers should be sampled sparingly, if at all; those determinations should in turn be guided by ichnological, paleontological, and sedimentological criteria (Gaines and Droser 2010). Such an approach is an effective balance between time, cost, and scientific merit; mitigates the mixing of the geochemical signal where it is most important; and demonstrates the effectiveness of geochemical techniques in paleoredox interpretations.

4.6.3 The relationship between redox and exceptional fossil preservation:

Exceptionally preserved biotas are relatively common in the Neoproterozoic-Cambrian compared to the remainder of the fossil record (Butterfield 2003). Multiple taphonomic pathways are known to have occurred during this time period, but none are more strongly linked to Cambrian shales than Burgess-Shale-type (BST) preservation. BST preservation is defined as the preservation of nonmineralizing organisms as carbonaceous compressions in shales (Butterfield 1995), and demonstrate a bias toward recalcitrant extracellular structures—jaws, cuticles, chetae—that are found in arthropods, polychaetes, and priapulid worms (Butterfield 2003). BST preservation is arguably the most ecologically significant method of fossil preservation in geologic history: our understanding of early animal evolution would certainly be much poorer without it.

The exceptional degree of preservation evident in BST benthic faunas—which include those preserved in the Spence, Wheeler, and Maotianshan Shales—offers paleontologists the greatest opportunity for understanding early animal evolution and ecology at a critical period in the history of life. Numerous models of BST preservation have been proposed, including the role of clay minerals (Butterfield 1995); the actions of Fe-reducing bacteria (Petrovich 2001); combination of anoxia, sulfate reduction, and low substrate permeability (Gaines et al. 2005); and the presence of hypersaline brines (Powell et al. 2003). In nearly all models of BST preservation, anoxic bottom water conditions are considered a basic prerequisite (Conway Morris 1986; Butterfield 1995; Petrovich 2001; Butterfield 2003; Gaines et al. 2005; Gaines and Droser 2010). In most

interpretations, BST faunas are presumed transported from an oxygen-rich habitat into the anoxic depositional environment for final burial and preservation (Gaines and Droser 2010).

The interpretation that BST faunas were transported prior to final burial imposes several limitations on the types of information that can be gleaned from a paleoecological study of these communities:

- 1) Multiple separate communities may be mixed during transport and burial. As a result community-scale analyses, such as analysis of relative abundance (Dornbos and Chen 2008) or comparative ecology between communities (Dornbos et al. 2005), may not accurately reflect true relationships between benthic taxa.
- 2) BST faunas appear only to have been transported short distances (Gaines et al. 2005). If so, BST faunas were likely living adjacent to near anoxic or anoxic conditions in stressed environmental settings, and therefore are not accurate representations of normal marine benthic communities (Gaines and Droser 2010).
- 3) BST faunas are not preserved *in situ*. Any interpreted relationships between the depositional environment in which they are preserved and the ecology and morphological adaptations to that environment are false (Dornbos et al. 2005; Kloss et al. 2009; Domke and Dornbos 2010).

There is a growing body of evidence to suggest that part or all members of BST faunas were preserved *in situ*. The Chengjiang biota as a whole is generally considered to represent an autochthonous assemblage: many infaunal forms within this fauna are found still preserved within their burrows (Chen and Zhou 1997), and specimens of the epifaunal cancelloriid *Allonnia phrixothrix* have been preserved *in situ*, their basal end embedded into and oriented perpendicular to bedding (Kloss et al. 2009). In the Burgess Shale, an examination of 15 species from the Greater Phyllopod Bed by Caron and Jackson (2006) concluded that the majority of specimens were preserved *in situ* and that any disturbance due to transport was minimal. Schlottke (2008), upon examination of samples of the Wheeler Shale, discovered a number of specimens of the eocrinoid *Gogia spiralis* apparently preserved *in situ*, with their stalks still embedded into and oriented perpendicular to the bedding plane.

Geochemical data has raised the possibility that a number of BST localities were capable of supporting an *in situ* fauna. The redox geochemistry of the Burgess Shale (Powell et al. 2003; Powell 2009) indicates a continuous record of oxic bottom water conditions, in stark contrast to our traditional picture of the Burgess Shale. Handle and Powell (2010) found oxic-to-anoxic fluctuations in the redox conditions of the Wheeler Shale. This treatment of the Wheeler and Spence Shale show a more consistent oxic-to-slightly-dysoxic character for redox conditions at both of these localities. Even ichnological models of the Wheeler and Spence suggest fluctuations between oxic and dysoxic-to-anoxic conditions (Garson et al. 2008; Gaines and Droser 2010). Finally, geochemical analysis of the Emu Bay Shale indicates deposition under oxic conditions

(McKirdy et al. 2011). In more than one study, at more than one locality, preservation of BST faunas appear to be preserved in beds associated with well-oxygenated shales, despite the necessary requirement of anoxic conditions to explain the taphonomic mechanisms behind BST preservation.

The application of these geochemical techniques in the realm of paleoecology and paleoenvironmental studies is in its relative infancy, and the effectiveness and utility of paleoredox analysis is still disputed by some workers (see previous section addressing the concerns of Gaines and Droser 2010). However, the use of geochemical redox proxies is not new. Petroleum geologists have been successfully applying these techniques to fine-grained siliciclastics for decades (Ernst 1970; Bjorlykke 1974; Dill 1986; Dill et al. 1988; Calvert and Pedersen 1993). Powell (et al. 2003; 2009) and Kimura and Watanabe (2001) have demonstrated with particular effectiveness several redox proxies and elements for use with Cambrian units. At the time of publication, Gaines and Droser (2010) pointed to two geochemical studies that address paleoredox in BST deposits, both in the Burgess Shale (that of Powell et al. 2003 and Hammarlund 2007); numerous more recent studies (that of Powell 2009, Handle and Powell 2010, McKirdy et al. 2011) have been added to a growing list of geochemical analyses that includes the work presented here that demonstrate consistency in geochemical results across a number of BST localities.

If the paleoenvironmental conditions associated with BST faunas indicate that many were deposited under well-oxygenated conditions, then what to do about the

proposed mechanisms for BST preservation that require anoxic conditions for operation? For example, Gaines et al. (2005) postulates that BST preservation in the Wheeler Shale resulted from a combination of three separate mechanisms: 1) low initial porosity of the substrate due to the physical nature of the carbonate-clay sediment; 2) reduced porosity due to deflocculation of clays under anoxic conditions; and 3) reduced permeability due to sealing of the substrate surface by precipitation of carbonate cement via sulfate reduction. Clearly, this model would not be able to operate in oxygen-rich depositional environments. In light of a growing body of geochemical data, any proposed model or mechanisms in the depositional environment explaining BST preservation should be able to account for the following observations: 1) oxic depositional conditions; 2) low bioturbation levels; 3) a taphonomic window for BST preservation that closes rapidly by the end of the Cambrian; and 4) the universal nature of BST preservation (i.e. exceptional preservation of recalcitrant extracellular tissue as flattened carbonaceous compressions; see Butterfield 2003).

Multiple hypotheses compatible with oxic depositional conditions have been put forth to account for the unique taphonomy in BST faunas: 1) obrution events, which have been implicated in nearly all BST faunal deposits (Seilacher et al. 1985; Liddell et al. 1997; Babcock et al. 2001); 2) fluctuating salinity conditions in the Maotianshan Shale that inhibited biodegradation in the Chengjiang Biota (Babcock et al. 2001); 3) injection of hypersaline pore waters from neighboring brine pools into the substrate, restricting biodegradation in the Burgess Shale and Kinzers Formation (Powell 2009); 4) unusually low levels of predation in the Kinzers Formation (Skinner 2005); and 5) the presence of

microbial mat cover in the Burgess (Powell et al. 2003) and Emu Bay Shales (McKirdy et al. 2011).

The role of obrution events in exceptional fossil preservation is a concept touted even in introductory geosciences courses, but such deposits are ubiquitous throughout the Phanerozoic fossil record and are not unique to the Cambrian taphonomic window. The lack of bioturbation may play a significant role in Cambrian obrution deposits by preventing biological degradation through bioerosion or re-exhumation (Skinner 2005); indeed, similar obrution deposits with moderate-to-intense levels of bioturbation from the early-to-middle Paleozoic do not exhibit BST preservation (Brett and Zambito IV 2012). However, Butterfield (1995) points out that enzymatic degradation of organic matter occurs regardless of bioturbation, and that earlier unbioturbated Ediacaran deposits, which are sedimentologically equivalent to Cambrian deposits, generally lack associated BST preservation. Similarly, unusually low predation pressure does not account for the lack of microbiological or enzymatic degradation of organic remains. Fluctuations in salinity can lead to the development of stressed marine environments and restricted normal faunal activity, promoting Proterozoic-like conditions even in modern depositional settings (i.e. Shark Bay, Australia; see Skyring and Bauld 1990). Currently this hypothesis is only being considered for shallow water Chengjiang Biota (Babcock 2001). Powell's hypersaline brine pool model (2009) neatly explains the abundance of fossil materials in the Burgess and Kinzers formations as the result of an ample supply of nutrient-rich brine waters delivered to local faunas, and further suggests that injections of hypersaline water into sediment pore spaces restricted

typical biodegradation and promoted BST preservation. These brine seeps are inferred from the presence of herringbone calcite and zoned quartz (Powell 2009), unusual diagenetic minerals not observed in Maotianshan, Wheeler, Spence, or Emu Bay Shales; Powell (2009) notes that not all BST deposits feature these minerals, citing the Marjum and Wheeler formations as examples. Hypersalinity, then, does not appear to be a universal model for BST preservation.

The microbial mat model of BST preservation is intriguing. Powell et al. (2003) hypothesized the presence of microbial mats in the Burgess Shale to explain BST preservation, though this suggestion was speculative and based on general knowledge of Cambrian siliciclastic settings rather than direct evidence of microbial colonization of the Burgess substrate. McKirdy et al. (2011) observed that the minimally bioturbated siliciclastic muds of the Emu Bay Shale were deposited beneath an oxic water column in association with sedimentary fabrics suggestive of microbial colonization. An earlier study of the Emu Bay Shale by the same research group determined that a significant fraction of preserved organic matter within the deposit is derived from cyanobacteria (McKirdy et al. 2011). From these results McKirdy et al. (2010) concluded that BST preservation in the Emu Bay Shale was aided by the presence of microbial mats in the substrate.

Many aspects of microbial mat communities mirror the criteria necessary for exceptional fossil preservation. Microbial mat cover is an effective “seal” on substrates, restricting geochemical exchange between the overlying water column and the

substrate, preventing the flow of oxygen-rich marine waters to sediment pore space and resulting in anoxic subsurface conditions. Sulfate-reducing bacteria, present in many microbial mat communities (Baumgartner et al. 2006) produce hydrogen sulfides, rendering the subsurface environment hostile to normal marine infauna. This reducing environment is absent of either oxygen or sulfate, the two most effective oxidizing agents associated with the decay of organic matter (Gaines and Droser 2010), and the biological activities of members of the mat community may promote chemical reactions that further enhance preservation: for example, sulfate reduction under anoxic conditions results in precipitation of calcium carbonate and early lithification of microbial mats (Baumgartner et al. 2006). The substrate environment presumably created by microbial mat communities in Cambrian shales is uncannily similar to the proposed taphonomic model of Gaines et al. (2005). The embryonic nature of Proterozoic-style sediments would have resulted in low initial porosity (Gaines et al. Criterion 1). The sealing of sediments by microbial mats further reduces porosity (Criterion 2). Finally, the activity of sulfate-reducing bacteria forces the precipitation of calcium carbonate and leads to porosity occlusion (Criterion 3), arresting microbial decay of nonmineralizing tissues and facilitating exceptional fossil preservation (Gaines et al. 2005). Since microbial mats prevent exchange between the substrate and overlying water column, this taphonomic process could take place even in dominantly oxic depositional settings.

As previously discussed, microbial mats were a common component of Neoproterozoic-Cambrian shallow subtidal marine environments, and their existence in

Cambrian shales that preserve BST faunas has been repeatedly hypothesized (Powell et al. 2003; Parsley and Prokop 2004; Dornbos et al. 2005; Kloss et al. 2009; Domke and Dornbos 2010; McKirdy et al. 2011). Microbially mediated substrates appear to be a near-universal component of minimally bioturbated Cambrian deposits, and persisted in normal marine settings in the absence of a burrowing fauna (Seilacher and Pflüger 1994). The demise of microbially mediated normal marine substrates is correlative to increasing intensity of bioturbation through the Phanerozoic during the agronomic revolution, and this event is coincident with the closing of the BST taphonomic window by the end of the Cambrian (Butterfield 2003). It would seem that the loss of microbial mats and their preservation-enhancing biomechanical properties would have deleterious effects on fossil preservation; thus the disappearance of BST preservation at the same time as the agronomic revolution would support the role of microbial mats in exceptional fossil preservation during the Cambrian.

While Proterozoic-style substrates and their associated microbial communities are generally absent from normal marine settings following the agronomic revolution, there are notable reoccurrences of Proterozoic-style substrates during the Triassic recovery from the end-Permian mass extinction (Pruss et al. 2004) and this periods are potential testing ground for this microbial mat hypothesis of exceptional preservation. BST preservation is not currently known from any localities of early Triassic age. It is unclear how the stressed nature of post-extinction marine environments, particularly the prolonged end-Permian recovery, may affect the preservation of BST faunas despite the resurgence of microbial communities.

Similarly, microbial mats have a long record in the Proterozoic (see Table 1 of Gehling (1999) for a fairly comprehensive list) and have been implicated in the preservation of the Ediacaran fauna in both coarse- and fine-grained sediments (Gehling 1999; LaFlamme et al. 2011), and are associated with “Bitter Springs”-type preservation in the Neoproterozoic (Butterfield 2003); while these taphonomic processes are distinctly different from BST preservation they do demonstrate how microbial mat communities may play a role in taphonomic processes and can operate within multiple preservational pathways. BST preservation is not known in the Proterozoic; this should come as no surprise, since the taphonomic process preserves structures—jaws, cuticle, chetae—that do not evolve in animals until the early Cambrian, even if animals were present earlier.

The microbial mat model for BST preservation is best supported by mineralogical and geochemical evidence in the Emu Bay Shale (McKirdy et al. 2011). Some evidence for microbially mediated substrates is also found in the Spence and Wheeler Shales (see previous chapter) as well as the Maotianshan Shale (Dornbos et al. 2005), though the overall body of evidence will be less than convincing for some workers. Definitive evidence for microbial mat colonization among BST depositional environments will be a crucial test of the microbial mat model hypothesis. Toward that end it is suggested that geochemical work continue in the Spence and Wheeler Shales: 1) focusing on paleoredox conditions in BST faunal beds; and 2) focusing on biomarker analysis of organic matter indicative of cyanobacterial occupation. As the geochemical evidence continues to mount, traditional “anoxic” taphonomic models will become increasingly

difficult to justify, and innovative new hypotheses like the microbial mat model will be necessary to account for exceptional fossil preservation taking place in well-oxygenated Cambrian shales.

4.7 Conclusions

The geochemical analysis of the Spence and Wheeler Shales demonstrates that:

- 1) The overall depositional setting of both Spence and Wheeler Shales were well-oxygenated;
- 2) The lack of correlation between redox and ichnofabrics suggest that bioturbation levels and substrate conditions developed independent of redox conditions;
- 3) The lack of correlation between redox and ichnofabrics suggest that both shales were dominated by Proterozoic-style substrates;
- 4) Scale effects of geochemical sampling are not significant in controlling or obscuring paleoredox values in the Spence Shale, and may be mitigated through proper sampling methodologies that focus on bedding planes of greatest interest;
- 5) Models of BST preservation in Cambrian Shales must account for the oxygenated depositional environments evidenced by a growing body of geochemical studies;

- 6) Microbial mat communities hosted the necessary geochemical conditions to promote BST preservation in oxygenated environments, representing a potential new model for exceptional fossil preservation during the Cambrian.

CHAPTER 5: CONCLUSIONS

A multidisciplinary approach incorporating sedimentological, paleoecological, and geochemical techniques to study the Spence, Wheeler, and Maotianshan Shales has revealed important new insights into the general paleoenvironmental conditions present during a period of significant geo-biological upheaval in Earth's history. In the second chapter a detailed mm-scale analysis of ichnofabrics revealed that both the Spence and Wheeler Shales are characterized by a lack of bioturbated substrates (avg. $\lambda = 1$ in Spence, $\lambda = 1$ in Wheeler). Maximum bioturbation intensity never exceeds the minimum threshold for mixed layer development, suggesting that Phanerozoic-style substrates were rare or absent and that Proterozoic-style substrates dominated the depositional environments of the Spence, Wheeler, and Maotianshan Shales. The presence of wavy-crinkly laminae and the evidence for cohesive behavior in both shales indicates that microbial mat communities played a role in the development of Proterozoic-style substrates, consistent with expectations for the agronomic revolution (Seilacher and Pflüger 1994). These results mimic earlier ichnofabric studies of the Maotianshan Shale (Dornbos et al. 2005; Kloss et al. 2009) and the Chisholm Shale (Domke and Dornbos 2010), suggesting that Proterozoic-style substrates were still common in certain depositional settings during the early-to-middle Cambrian. From these results one can hypothesize that most benthic taxa living on substrates

represented by these shales should exhibit Proterozoic-style adaptations to substrate conditions.

This chapter also highlights some potential difficulties regarding the use of ichnofabric vs. ichnofacies models for paleoenvironmental interpretations of Cambrian shale units. While ichnofabric models are focused on interpretations of substrate character independent of redox conditions in the overlying bottom water, ichnofacies models target redox conditions independent of substrate character. While these interpretations are not mutually exclusive, they will complicate paleoecological interpretations of preserved benthic faunas. While ichnofacies models are effective for the vast majority of the Phanerozoic, it must be recognized that the unusual nature of Cambrian substrates may dictate priority to ichnofabric analogues for paleoenvironmental interpretation. Since Proterozoic-style substrates can develop under both oxic and anoxic conditions, sedimentological analysis alone may not be adequate to determine redox conditions for certain Cambrian depositional settings.

In the third chapter morphological adaptations for individual benthic taxa are compared across marine communities preserved in Burgess-Shale-type (BST) Lagerstätte for interpretation of paleoenvironmental conditions in lieu of sedimentological evidence. Genus-level analysis of morphological adaptations indicates that Cambrian benthic communities contained a mix of Proterozoic- and Phanerozoic-style adaptive strategies. The substrates in which these marine communities lived had reached a transitional phase between end-member-substrate-style dominance by the early-to-

middle Cambrian. These observations are consistent with expectations for the agronomic revolution. The agronomic and Cambrian substrate revolutions were globally synchronous events that led to the development of mixed-morphology benthic marine communities distinct from both pre- and post-Cambrian faunas that evolved under the dominant regime of one or the other end-member-substrate-styles. A further attempt is made to quantify the association between Phanerozoic- and Proterozoic-style substrates (through the creation of the Substrate Adaptability Index; SAI) to track the progression of the agronomic and Cambrian substrate revolutions through time, but the results from this effort are somewhat inconclusive. This is likely due to the simple nature of the SAI calculation, which does not account for environmental factors or the differences in adaptive flexibility between Phanerozoic- and Proterozoic-style substrates.

The paleoecological results compare favorably with sedimentological analysis for the Maotianshan, Spence, and Wheeler Shales, suggesting that substrates on which these benthic faunas lived were indistinguishable from the substrates found in all three shales. Evidence for *in situ* preservation of the benthic fauna has been observed in the Maotianshan (Chen and Zhou 1997; Kloss et al. 2009) and the Wheeler Shale (Gaines and Droser 2003; Schlottke 2008), and field observations of preserved articulated chancelloriids and gogiids from both the Spence and Wheeler Shales suggests *in situ* or minimal transport conditions. In short, it is likely that the benthic faunas in all three shales were preserved in the substrates in which they were living. Thus, the local redox

conditions must have been sufficient to support benthic metazoans living on the substrate.

The fourth chapter introduces geochemical techniques to resolve the issue of redox conditions associated with the deposition of Cambrian shales. Geochemical analysis using the paleoredox indices V/Cr and $V/(V+Ni)$, and the enrichment factors V , Cr , Ni , and Zn , indicate that the Spence and Wheeler Shales were deposited under predominantly oxic conditions. A cursory geochemical analysis of the Maotianshan Shale also indicates oxygenation of the water column. A comparison of geochemical results to the ichnofabric analyses from the second chapter suggests that redox conditions operated relatively independently of changes in bioturbation levels in the Spence and Wheeler Shales. The lack of bioturbated substrates in the Spence, Wheeler, and Maotianshan Shales cannot be driven by redox conditions, but instead must be accounted for by some other environmental constraint; the most likely explanation is that all three shales were dominated by Proterozoic-style substrates inhibiting the activity of burrowing organisms in oxygenated settings. This hypothesis is internally consistent between sedimentological, paleoecological, and geochemical observations made at all three shales, and is consistent with the expectations of the agronomic revolution.

The use of geochemical analysis also highlights the limitations of ichnofabric/facies model as applied to Cambrian settings. Environments traditionally interpreted as having been anoxic using ichnofacies are clearly not according to

geochemistry. The ichnofabric index is slightly more robust in face of the geochemical signal since (ii)-fabrics are not directly concerned with redox; but since (ii)-fabrics are often applied to paleoecological studies of associated faunas, it is easy to see how ignorance of the “true” redox signal may lead to erroneous interpretations. In light of these considerations, it is suggested here that geochemical techniques should be incorporated with more traditional sedimentological and paleontological approaches in studies of early-middle Cambrian depositional environments.

The revelation that many Cambrian environments once thought of as anoxic are in fact well oxygenated has far reaching implications for paleontological studies concerning this period. For one, Cambrian shales were capable of *in situ* development of marine communities, which offers strong support to paleoecological interpretations that rely upon *in situ* preservation of fauna (Parsley and Prokop 2004; Dornbos et al. 2005; Kloss et al. 2009; Domke and Dornbos 2010). Second, the presence of a well-oxygenated water column requires the rethinking of current hypotheses regarding the development of BST preservation during the Cambrian. Since most current models of BST preservation require anoxia, a new generation of ideas concerning exceptional fossil preservation will have to be developed to account for the slew of geochemical data now being produced. A new model is proposed here that suggests that microbial mats can create the necessary geochemical conditions that may lead to BST preservation in oxygenated marine environments. The ubiquity of microbial mats in marine environments account for the occurrence of BST preservation under disparate depositional conditions, and the loss of mats concurrent with the agronomic revolution coincides with the disappearance

of BST taphonomic windows by the end Cambrian. Microbial mats are known, suspected, or hypothesized to have lived in most Cambrian shales with BST faunas, and additional geochemical studies should focus on bedding planes hosting BST faunas to confirm the redox conditions and attempt to identify biomarkers associated with the presence of cyanobacteria.

The geochemical techniques utilized here are also broadly applicable to geologic periods beyond the Cambrian and may aid in interpretation of other nonactualistic marine settings. For example, microbial mats had a resurgence in shallow subtidal marine settings in the wake of the late Ordovician and end-Permian biotic crises (Sheehan and Harris 2002; Pruss et al. 2004), and geochemical analyses may again be put to use in paleoenvironmental interpretations. These post-crisis intervals may also be useful in testing the microbial mat hypothesis for exceptional preservation by predicting that if BST preservation reoccurs at all, it will be during the recovery intervals of such biotic crises.

The results of this work have shed new light on critical environmental aspects of Cambrian depositional settings, demonstrated the effectiveness of combining traditional paleontological approaches with geochemical techniques, redefined our understanding of the relationships between Cambrian substrates and redox conditions, and should cause us to reconsider our view of important ecological and taphonomic processes associated with a significant period of biological development in the history of life. It is hoped that future studies derived from the material presented here will further clarify

the roles of environmental, taphonomic, and paleoecological relationships during the Cambrian radiation.

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APPENDIX A

Ichnofabric index data for Wheeler and Spence Shales.

Specimen	Total count (mm)	ii1	ii2	ii3	ii4	ii5	Notes
W1A	32	30	0	2	0	0	
W1B	65	60	0	5	0	0	
W1C	33	26	6	0	0	0	
W1D	31	31	0	0	0	0	
W1E	44	39	5	0	0	0	
W1F	14	11	3	0	0	0	
W1G	9	9	0	0	0	0	
W1HI	37	37	0	0	0	0	
W1J	23	21	2	0	0	0	fold over structure
W1K	30	30	0	0	0	0	
W1L	30	27	3	0	0	0	
W1N	18	18	18	0	0	0	
W1O	36	36	0	0	0	0	
SUBTOTAL	402	375	37	7	0	0	
W2B	25	25	0	0	0	0	
W2C	33	30	3	0	0	0	
W2D	38	34	0	4	0	0	

W2E	37	37	0	0	0	0	
W2F	42	40	2	0	0	0	
W2G	36	36	0	0	0	0	
W2H	14	14	0	0	0	0	
W2I	27	24	3	0	0	0	
W2J	21	21	0	0	0	0	
SUBTOTAL	273	261	8	4	0	0	
W3B	40	38	2	0	0	0	
W3C	60	44	0	16	0	0	
W3D	30	30	0	0	0	0	
W3E	64	61	0	3	0	0	
SUBTOTAL	194	173	2	19	0	0	
W4A	28	28	0	0	0	0	
W4B	21	21	0	0	0	0	
W4C	23	23	0	0	0	0	
W4D	39	39	0	0	0	0	
SUBTOTAL	111	111	0	0	0	0	
W5A	70	70	0	0	0	0	
W5B	29	18	11	0	0	0	
W5C	23	21	2	0	0	0	
W5D	28	28	0	0	0	0	
W5E	30	17	13	4	0	0	
W5F	17	17	0	0	0	0	

W5G	25	23	2	0	0	0	
W5H	25	19	3	3	0	0	burrows @ 15-18mm
SUBTOTAL	247	213	31	7	0	0	
W6A	53	53	0	0	0	0	
W6B	19	16	3	0	0	0	
W6C	31	28	3	0	0	0	
W6D	28	23	0	5	0	0	
SUBTOTAL	131	120	6	5	0	0	
W7A	69	66	3	0	0	0	
W8A	38	36	2	0	0	0	
WHEELER SUBTOTAL	1485	1370	72	44	0	0	
LMH1A	35	35	0	0	0	0	
LMH1B	30	30	0	0	0	0	
LMH1C	28	28	0	0	0	0	
LMH1D	43	43	0	0	0	0	
LMH1E	45	45	0	0	0	0	
LMH1F	29	25	4	0	0	0	
LMH1G	30	39	1	0	0	0	
MH1A	15	12	3	0	0	0	
MH1B	54	54	0	0	0	0	
MH1C	31	29	2	0	0	0	
MH1D	26	20	3	3	0	0	

MH1E	10	10	0	0	0	0	
MH1F	36	32	4	0	0	0	
MH1G	29	29	0	0	0	0	
SUBTOTAL	441	431	17	3	0	0	
LMH2A	50	48	2	0	0	0	
LMH2B	44	41	3	0	0	0	
LMH2C	30	30	0	0	0	0	
LMH2D	28	28	0	0	0	0	remnant mat?
LMH2E	49	44	3	2	0	0	
LMH2F	49	44	2	3	0	0	
SUBTOTAL	250	235	10	5	0	0	
LMH3A	32	32	0	0	0	0	
LMH3B	37	37	0	0	0	0	roll-up structure
LMH3C	23	23	0	0	0	0	
LMH3D	26	26	0	0	0	0	
LMH3E	51	46	5	0	0	0	
LMH3F	27	23	4	0	0	0	
MH3G	22	22	0	0	0	0	
LMH3H	25	25	0	0	0	0	
LMH3I	21	21	0	0	0	0	
LMH3J	32	29	3	0	0	0	
LMH3K	31	26	5	0	0	0	
SUBTOTAL	327	310	17	0	0	0	

LMH4A	33	33	0	0	0	0	
LMH4B	16	16	0	0	0	0	
LMH4C	23	23	0	0	0	0	
LMH4D	54	50	4	0	0	0	
SUBTOTAL	126	122	4	0	0	0	
MC4A	32	32	0	0	0	0	
MC4B	62	58	4	0	0	0	
MC4C	69	63	5	1	0	0	
MC4D	57	50	4	3	0	0	
SUBTOTAL	220	203	13	4	0	0	
MC6	49	49	0	0	0	0	
MC7A	54	54	0	0	0	0	
MC7B	67	58	9	0	0	0	
MINERS HOLLOW SUBTOTAL	1534	1462	70	12	0	0	
ON1	91	91	0	0	0	0	
ON2	96	96	0	0	0	0	
ON3	117	117	0	0	0	0	
ON4	154	154	0	0	0	0	
ON5	102	102	0	0	0	0	
ON6	85	85	0	0	0	0	
SUBTOTAL	644	644	0	0	0	0	
ONA	41	41	0	0	0	0	
ONB	63	63	0	0	0	0	

ONC	26	26	0	0	0	0	
OND	47	47	0	0	0	0	
ONEIDA NARROWS SUBTOTAL	821	821	0	0	0	0	
SG1A	100	100	0	0	0	0	
SG2A	46	46	0	0	0	0	
SG2B	62	62	0	0	0	0	
SG3A	58	58	0	0	0	0	
SG3B	54	54	0	0	0	0	
SPENCE GULCH SUBTOTAL	320	320	0	0	0	0	
HC1A	17	3	3	0	11	0	
HC1B	23	3	20	0	0	0	
HC1C	12	12	0	0	0	0	
HC2A	62	8	5	41	8	0	
HC2B	25	22	3	0	0	0	
HC2C	72	10	62	0	0	0	
HIGH CREEK SUBTOTAL	211	58	93	41	19	0	
SPENCE SUBTOTAL	2883	2646	160	58	19	0	
TOTAL	4330	4016	232	102	19	0	

APPENDIX B

Substrate Adaptability Index Data

Maotianshan Shale	(modified from Dornbos et al. 2005)	520-516 Ma	
			See Dornbos et al. 2005 for detailed analysis
# Proterozoic:	17		
# Phanerozoic:	2		
SAI	0.11		
Burgess Shale	(modified from Dornbos et al. 2005)	513-500 Ma	
			<i>Scenella</i> (not initially reported in Dornbos et al. 2005); see reference for detailed analysis
# Proterozoic:	14		mat grazer
# Phanerozoic:	8		
SAI	0.38		
Indian Springs	(modified from English and Babcock 2010)	530-513 Ma	
# Proterozoic:	4	Helicoplacoid	sed sticker
		Chancelloriid	sed sticker
		<i>Mickwitzia</i>	sed rester
			sed rester/sticker (?)
		Obolleid	
# Phanerozoic:	0		
SAI	0.00		

Spence Shale	(modified from Robison 1991)	516-513 Ma
# Proterozoic:	5	<i>Choia</i> sed rester <i>Vauxia</i> sed sticker <i>Scenella</i> mat grazer <i>Chancelloria</i> sed sticker <i>Wiwaxia</i> mat grazer
# Phanerozoic:	7	hard substrate attacher hard substrate attacher <i>Diraphora</i> hard substrate attacher <i>Gogia</i> hard substrate attacher <i>Micromitra</i> benthic deposit feeder <i>Cruziana</i> <i>Lingulella</i> infaunal <i>Acrothele</i> infaunal
# Unknown:	2	<i>Ctenocystis</i> <i>Protospongia</i>
SAI	0.58	

"Shallow" Wheeler	(modified from Robison 1991)	513-500 Ma
# Proterozoic:	5	<i>Vauxia</i> sed sticker
		<i>Latouchella</i> mat grazer
		<i>Pelagiella</i> mat grazer
		<i>Gogia spiralis</i> sed sticker
		<i>Chancelloria</i> sed sticker
		hard substrate attacher
# Phanerozoic:	6	<i>Micromitra</i> hard substrate attacher
		<i>Nisusia</i> hard substrate attacher
		<i>Rusophycus</i> benthic deposit feeder
		<i>Acrothele</i> infaunal
		<i>Lingulella</i> infaunal
		<i>Treptichnus</i> benthic deposit feeder
# Unknown:	2	<i>Ctenocystis</i>
		<i>Stenothecoides</i>
SAI	0.55	
"Deep" Wheeler	(modified from Robison 1991)	513-500 Ma
# Proterozoic:	7	<i>Choia</i> sed rester

		<i>Diagonella</i>	sed sticker
		<i>Latouchella</i>	mat grazer
		<i>Melopegma</i>	mat grazer
		<i>Gogia spiralis</i>	sed sticker
		<i>Chancelloria</i>	sed sticker
		<i>Allonnia</i>	sed sticker
			hard substrate attacher
# Phanerozoic	5	<i>Acrothele</i>	
		<i>Linnarssonina</i>	infaunal
		<i>Micromitra</i>	infaunal
		<i>Prototreta</i>	infaunal
			hard substrate attacher
		<i>Nisusia</i>	
# Unknown:	2	<i>Sentinella</i>	
		<i>Kiwetinokia</i>	
SAI	0.42		
Marjum Formation	(modified from Robison 1991)		513-500 (Ma)
# Proterozoic:	7	<i>Choia</i>	sed rester
		<i>Vauxia</i>	sed sticker
		<i>Diagonella</i>	sed sticker
		<i>Latouchella</i>	mat grazer

		<i>Totiglobus</i>	sed attacher
		<i>Chancelloria</i>	sed sticker
		<i>Aysheaia</i>	mat walker
		<i>Marjumicystites</i>	sed sticker
# Phanerozoic	7	<i>Acrothele</i>	infaunal
		<i>Lingulella</i>	infaunal
		<i>Micromitra</i>	hard substrate attacher
		<i>Nisusia</i>	hard substrate attacher
		<i>Linnarssonina</i>	infaunal
		<i>Pegmatreta</i>	infaunal
		<i>Prototreta</i>	infaunal
# Unknown:	4	<i>Valospongia</i>	
		<i>Hamptonia</i>	
		<i>Hazelia</i>	
		<i>Castericystis</i>	
SAI	0.50		
Kinzers Formation	(PALEO DB)		516-513 Ma
# Proterozoic:	9	<i>Leptomitius</i>	sed sticker
		<i>Lepitocyttis</i>	sed sticker
		<i>Kinzercystis</i>	sed attacher

		<i>Camptostroma</i>	sed sticker
		<i>Chancelloria</i>	sed sticker
		<i>Yochelcionella</i>	mat grazer
		<i>Pelagiella</i>	mat grazer
		<i>Planutenia</i>	mat grazer
		<i>Byronia</i>	sed sticker
# Phanerozoic:	5	<i>Nisusia</i>	hard substrate attacher
		<i>Kurtogina</i>	hard substrate attacher
		<i>Eoobolus</i>	infaunal
		<i>Eothele</i>	infaunal
		<i>Hadrotreta</i>	infaunal
# Unknown:	1	<i>Protospongia</i>	
SAI	0.36		
Sirius Passet (Buen)	(PALEO DB)		520-516 Ma
# Proterozoic:	2	<i>Choia</i>	sed rester
		<i>Halkieria</i>	mat grazer
# Phanerozoic:	0		

Unknown: 2 *Hadranax*
Buenaspis

SAI 0.00

Pioche Shale (PALEO DB) 516-513

Proterozoic: 0

Phanerozoic: 4 *Eothele* infaunal
Obulus infaunal
Micromitra hard substrate attacher
Cruziana deposit feeder

Unknown: 0

SAI 1.00

Chisholm Shale (PALEO DB) 513-500 Ma

Proterozoic: 2 *Totiglobus* sed attacher
Gogia longidactylus sed sticker

Phanerozoic: 0

Unknown:

SAI		0.00	
Latham Shale	(PALEO DB)		516-513 Ma
# Proterozoic:		0	
# Phanerozoic:		1	<i>Gogia</i> hard substrate attacher
# Unknown:		0	
SAI		1.00	
Mount Cap	(PALEO DB)		530-515 Ma
# Proterozoic:			<i>Chancelloria</i> sed sticker
			<i>Wiwaxia</i> mat grazer
# Phanerozoic:			<i>Micromitra</i> hard substrate attacher
# Unknown:			<i>Protospongia</i>
SAI		0.33	
Parker Slate	(PALEO DB)		530-513 Ma

# Proterozoic:	4	<i>Leptomitius</i>	sed rester
		<i>Chancelloria</i>	sed sticker
		<i>Coreospira</i>	mat grazer
		<i>Emmonsaspis</i>	sed attacher

# Phanerozoic:	3	<i>Eocystites</i>	hard substrate attacher
		<i>Nisusia</i>	hard substrate attacher
		<i>Wimanella</i>	hard substrate attacher

# Unknown:	0		
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SAI	0.43		
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Orsten	(C.O.R.E)	<i>Chancelloria</i>	late Cambrian
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Described as a "flocculent bottom layer"

SAI 0.7-0.9

Winneshiek	(Liu et al. 2006)		middle Ordovician
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lingulids abundant

SAI 1.0

Mistaken Point (PALEO BD)

# Proto	12	<i>Hiemalora</i>	560- 580Ma
		<i>Charniodiscus</i>	
		<i>Aspidella</i>	
		<i>Ivesheadia</i>	
		<i>Charnia</i>	
		<i>Primocandelabrum</i>	
		<i>Charnia</i>	
		<i>Bradgatia</i>	
		<i>Fractofusus</i>	
		<i>Thectardis</i>	
		<i>Beothukis</i>	
		<i>Pectifrons</i>	
Unknown	2	<i>Parviscopa</i>	
		<i>Hadrynichorde</i>	
SAI	0		

APPENDIX C
Geochemical Data

Appendix C. Geochemical data for the Wheeler Shale

Sample	Al (ppm)	V (ppm)	Ni (ppm)	Cr (ppm)	Zn (ppm)	EF (V)	EF (Ni)	EF (Cr)	EF (Zn)	V/Cr	V/(V+Ni)
Wedepohl	88900	130	68	90	95						
W1A	62660	39	30	64	61	0.42	0.63	1.01	0.92	0.60	0.56
W1C	58032	37	21	59	109	0.43	0.47	1.01	1.75	0.62	0.64
W1D	74308	48	27	91	106	0.44	0.48	1.21	1.34	0.53	0.64
W1H	69264	35	32	87	46	0.34	0.61	1.25	0.62	0.39	0.52
W1J	78936	57	33	80	86	0.50	0.55	1.00	1.02	0.72	0.63
W1K	69784	45	33	72	72	0.44	0.62	1.02	0.97	0.62	0.58
W1L	59176	41	27	80	70	0.47	0.60	1.34	1.11	0.51	0.60
W1O	54912	39	16	68	59	0.48	0.37	1.23	1.00	0.57	0.71
W2A1	46200	33	45	69	128	0.50	0.66	1.02	1.89	0.70	0.59
W2A2	50010	41	54	81	128	0.56	0.73	1.11	1.75	0.73	0.59
W2B	49020	39	53	73	121	0.55	0.74	1.02	1.68	0.77	0.58
W2C1	44320	25	41	63	129	0.38	0.63	0.97	1.99	0.58	0.54
W2C2	42488	39	59	60	118	0.62	0.95	0.96	1.91	0.93	0.56
W2D1	40232	35	63	58	79	0.60	1.08	0.99	1.34	0.88	0.52
W2D2	46910	41	36	63	98	0.60	0.52	0.91	1.43	0.95	0.69
W2E1	42676	42	49	69	73	0.67	0.79	1.10	1.16	0.88	0.62
W2E2	39245	48	46	67	67	0.83	0.80	1.17	1.17	1.02	0.66
W2F	44200	46	38	64	69	0.71	0.58	0.98	1.07	1.04	0.70
W2F2	40232	35	30	62	73	0.59	0.52	1.05	1.25	0.81	0.68
W2G1	48363	45	58	100	84	0.63	0.82	1.41	1.18	0.65	0.60
W2G2	44040	40	59	62	72	0.62	0.91	0.96	1.12	0.94	0.57
W2H	67116	75	58	83	101	0.77	0.59	0.85	1.03	1.31	0.71
W2I	69137	62	68	120	88	0.61	0.67	1.19	0.87	0.74	0.63
W5A1	34736	ND	ND	54	85	NA	NA	1.54	2.30	NA	NA
W5A2	30056	ND	ND	52	76	NA	NA	1.72	2.35	NA	NA
W5A3	32292	ND	ND	47	53	NA	NA	1.44	1.54	NA	NA
W5C	41236	ND	ND	57	60	NA	NA	1.37	1.36	NA	NA
W5D	56316	ND	ND	65	83	NA	NA	1.14	1.38	NA	NA
W5E	48256	ND	ND	55	58	NA	NA	1.14	1.12	NA	NA
W5F	52624	ND	ND	66	58	NA	NA	1.24	1.04	NA	NA
W5G	44044	ND	ND	54	98	NA	NA	1.21	2.08	NA	NA
W5H	38376	ND	ND	49	62	NA	NA	1.27	1.50	NA	NA
W5I	43992	ND	ND	64	68	NA	NA	1.43	1.45	NA	NA

Appendix C. Geochemical data for the Spence Shale

Sample	Al (ppm)	V (ppm)	Ni (ppm)	Cr (ppm)	Zn (ppm)	EF (V)	EF (Ni)	EF (Cr)	EF (Zn)	V/Cr	V/(V+Ni)
Wedepohl	88900	130	68	90	95						
LMH1A	116940	63	51	102	126	0.37	0.57	0.86	1.01	0.62	0.39
LMH1B	104622	86	34	81	66	0.56	0.42	0.77	0.59	1.07	0.57
LMH1C	103260	69	41	96	96	0.46	0.52	0.92	0.87	0.72	0.47
LMH1D	105750	60	29	96	78	0.39	0.36	0.90	0.69	0.63	0.52
LMH1E	107100	83	27	92	73	0.53	0.33	0.85	0.63	0.91	0.62
LMH1F	89958	62	40	65	403	0.47	0.58	0.71	4.19	0.96	0.45
LMH1G	100020	67	32	85	103	0.46	0.41	0.84	0.96	0.78	0.52
MH1B	96820	82	77	117	159	0.58	0.54	0.83	1.12	1.02	0.52
MH1C	90240	91	65	114	178	0.69	0.49	0.87	1.35	1.15	0.58
MH1D	95269	94	76	129	166	0.68	0.55	0.93	1.19	1.05	0.55
MH1E	98841	73	53	102	92	0.50	0.37	0.71	0.64	1.03	0.58
LMH2A	98852	40	46	127	115	0.28	0.61	1.27	1.08	0.32	0.46
LMH2B	100880	41	47	108	95	0.28	0.60	1.06	0.88	0.38	0.47
LMH2C	100412	41	44	110	114	0.28	0.57	1.08	1.06	0.37	0.48
LMH2D	97396	31	38	97	118	0.22	0.50	0.98	1.13	0.32	0.46
LMH2E	103376	51	43	95	116	0.34	0.54	0.91	1.05	0.54	0.55
LMH2F	97188	37	42	103	123	0.26	0.57	1.04	1.18	0.36	0.46
LMH2G	107848	38	44	96	104	0.24	0.53	0.88	0.90	0.40	0.47
LMH3AB	107588	39	46	91	110	0.24	0.56	0.84	0.96	0.42	0.46
LMH3CD	121368	36	40	107	109	0.20	0.43	0.87	0.84	0.34	0.47
LMH3E	112008	33	58	104	132	0.20	0.68	0.92	1.10	0.31	0.36
LMH3FG	113048	40	39	107	138	0.24	0.46	0.93	1.14	0.38	0.50
LMH3HI	110344	48	62	86	137	0.30	0.73	0.77	1.16	0.56	0.44
LMH3JK	107692	37	68	77	171	0.24	0.82	0.71	1.49	0.48	0.36
LMH4A	106600	42	41	102	120	0.27	0.50	0.94	1.06	0.42	0.51
LMH4B	110864	34	66	100	173	0.21	0.78	0.89	1.46	0.34	0.34
LMH4C	112476	39	40	104	120	0.24	0.46	0.92	1.00	0.37	0.49
LMH4D1	111488	33	40	97	104	0.20	0.47	0.86	0.87	0.33	0.45
LMH4D2	113568	33	47	94	124	0.20	0.54	0.82	1.02	0.36	0.42
LMH4E	111592	36	57	72	125	0.22	0.67	0.64	1.05	0.50	0.39

Appendix C. Geochemical data for the Spence Shale

Sample	Al (ppm)	V (ppm)	Ni (ppm)	Cr (ppm)	Zn (ppm)	EF (V)	EF (Ni)	EF (Cr)	EF (Zn)	V/Cr	V/(V+Ni)
Wedepohl	88900	130	68	90	95						
LMH2A1	92980	34	36	96	111	0.25	0.50	1.02	1.12	0.35	0.49
LMH2A2	92664	42	47	82	121	0.31	0.67	0.88	1.22	0.51	0.47
LMH2A3	98332	43	35	99	98	0.30	0.46	1.00	0.94	0.43	0.55
LMH2A4	100932	37	38	100	108	0.25	0.49	0.98	1.01	0.37	0.50
LMH2B1	98644	32	44	107	108	0.22	0.58	1.07	1.02	0.30	0.42
LMH2B2	97604	48	44	103	127	0.33	0.59	1.05	1.22	0.46	0.52
LMH2B3	96616	39	38	85	130	0.28	0.52	0.86	1.26	0.47	0.51
LMH2C1	97396	48	44	71	119	0.34	0.60	0.72	1.14	0.67	0.52
LMH2C2	97084	48	63	98	111	0.33	0.84	0.99	1.07	0.49	0.43
LMH2C3	96824	36	38	84	119	0.26	0.52	0.85	1.15	0.43	0.49
LMH2D1	101660	36	51	108	114	0.24	0.65	1.05	1.05	0.33	0.41
LMH2D2	100984	46	35	104	133	0.31	0.46	1.02	1.23	0.44	0.56
LMH2D3	103064	41	42	85	143	0.27	0.53	0.81	1.29	0.48	0.49
LMH2E1	97500	37	39	94	125	0.26	0.52	0.95	1.20	0.40	0.49
LMH2E2	92040	39	41	115	200	0.29	0.58	1.24	2.03	0.34	0.49
LMH2E3	95992	48	45	84	129	0.34	0.61	0.87	1.25	0.57	0.51
LMH2E4	101244	53	42	86	118	0.36	0.54	0.84	1.09	0.62	0.56
LMH2E5	98332	29	47	86	118	0.20	0.63	0.86	1.12	0.34	0.38
LMH2E6	102752	32	38	109	107	0.22	0.48	1.05	0.97	0.30	0.46
SG1A	115804	47	65	109	102	0.28	0.73	0.93	0.82	0.43	0.42
SG2A	124280	43	61	121	117	0.24	0.64	0.96	0.88	0.35	0.42
ON2A	122616	99	43	102	147	0.55	0.46	0.82	1.12	0.97	0.70
ON2B	121368	96	27	107	111	0.54	0.30	0.87	0.86	0.89	0.78
HC1A	115440	39	54	81	170	0.23	0.61	0.70	1.38	0.47	0.42
HC1B	122408	47	50	89	124	0.26	0.53	0.72	0.95	0.53	0.49
MC4	112424	52	40	104	88	0.32	0.47	0.91	0.73	0.50	0.57
MC6	110292	34	52	81	123	0.21	0.62	0.73	1.04	0.42	0.40
MC7	113724	39	61	85	137	0.23	0.70	0.74	1.13	0.46	0.39

Appendix C. Geochemical data for the Maotianshan Shale

Sample	Al (ppm)	V (ppm)	Ni (ppm)	Cr (ppm)	Zn (ppm)	EF (V)	EF (Ni)	EF (Cr)	EF (Zn)	V/Cr	V/(V+Ni)
Wedepohl	88900	130	68	90	95						
M3A	70460	89	84	66	73	0.86	1.56	0.93	0.97	1.35	0.51
M4A	64688	213	74	82	69	2.25	1.50	1.25	1.00	2.60	0.74
M4B	70200	150	86	100	65	1.46	1.60	1.41	0.87	1.50	0.64
M5C	68692	89	68	88	63	0.89	1.29	1.27	0.86	1.01	0.57
M6B	74984	105	71	91	59	0.96	1.24	1.20	0.74	1.15	0.60

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Publications and Presentations

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