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On the edge of exceptional preservation: insights into the role of redox state in Burgess Shale-type taphonomic windows from the Mural Formation, Alberta, Canada

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Abstract

Animals originated in the Neoproterozoic and 'exploded' into the fossil record in the Cambrian. The Cambrian also represents a high point in the animal fossil record for the preservation of soft tissues that are normally degraded. Specifically, fossils from Burgess Shale-type (BST) preservational windows give paleontologists an unparalleled view into early animal evolution. Why this time interval hosts such exceptional preservation, and why this preservational window declines in the early Paleozoic, have been long-standing questions. Anoxic conditions have been hypothesized to play a role in BST preservation, but recent geochemical investigations of these deposits have reached contradictory results with respect to the redox state of overlying bottom waters. Here, we report a multi-proxy geochemical study of the Lower Cambrian Mural Formation, Alberta, Canada. At the type section, the Mural Formation preserves rare recalcitrant organic tissues in shales that were deposited near storm wave-base (a Tier III deposit; the worst level of soft-tissue preservation). The geochemical signature of this section shows little to no evidence of anoxic conditions, in contrast to published multi-proxy studies of more celebrated Tier I and II deposits. These data help confirm that 'decay limited' BST biotas were deposited in more oxygenated conditions, and support a role for anoxic conditions in BST preservation. Finally, we discuss the role of iron reduction in BST preservation, including the formation of iron-rich clays and inducement of sealing seafloor carbonate cements. As oceans and sediment columns became more oxygenated and more sulfidic through the early Paleozoic, these geochemical changes may have helped close the BST taphonomic window.

Introduction

The Cambrian radiation of animal life represents the appearance of nearly every major animal phylum in the fossil record within a geologically rapid span of ~25 million years. The rapid increase in animal diversity and disparity is apparent in multiple records including the normal shelly fossil record (e.g. brachiopods, trilobites; (1)), the trace fossil record (2–4), phosphatized small shelly fossils (5–7) and small carbonaceous fossils (SCFs; (8,9)). The most celebrated archive of this event, though, is from Burgess Shale-type (BST) deposits, where primary organic tissues are preserved as thin carbonaceous films (see (10) for definitions). Critically, these lagerstätten preserve the soft parts of animals, and while the communities do not preserve a completely unbiased snapshot of early Cambrian life (for instance, size; (11)), they do provide our best glimpse of early metazoan ecosystems (12–15). Most important, by preserving most or all characters of an organism, fossils from BST biotas have been critical in understanding the polarity and order of morphological character evolution within each individual phylum (16).

The question of how organisms can escape the decay process, and why these BST lagerstätten appears to be concentrated in the Cambrian period—even after accounting for factors like rock outcrop area (17,18)—has long intrigued geologists. It was recognized early on that low oxygen levels (or complete anoxia) might play a prominent role in reducing decay. Actualistic decay experiments, however, established that decay under anoxic conditions (at least in the presence of normal marine sulfate levels) can still proceed rapidly (19,20). For soft-bodied deposits in general, then, anoxia mainly serves to 1) prevent scavenging, which would otherwise destroy carcasses (21), and 2) help induce the precipitation of authigenic minerals, which are involved in most exceptionally preserved deposits (22). In the most recent review of BST preservation (10), the window for abundant and exquisite BST fossil preservation is hypothesized to occur in a ‘goldilocks’ zone near where the chemocline (the point in the water column at which no oxygen remains) intersects the seafloor. At seafloor depths well below the chemocline, the setting is ‘supply limited’ in that animals cannot live in anoxic conditions, and carcasses simply cannot be supplied to these preservational settings through transport. Only preservation of nektonic/planktonic organisms falling through the water column could potentially occur. Conversely, at seafloor depths well above the chemocline, the setting is ‘decay limited’ (preservation limited) in that aerobic degradation and bioturbating organisms quickly destroy carcasses. Gaines (10) directly related the quality of preservation and species-level diversity of BST biotas to the position of these deposits along the spectrum from ‘supply limited’ to ‘decay limited’. The most spectacular deposits, such as the Burgess Shale and Chengjiang (Tier 1), are hypothesized to occur in the window where there is sufficient transport energy to carry soft-bodied benthic organisms across the chemocline into anoxic waters. Tier II deposits such as Kaili, Marjum and Spence lack sufficient transport energy or have source communities too far up-slope above the chemocline, and so it is dominantly hydrodynamically light organisms (e.g. algae) or dead carcasses that can be carried to the zone of exceptional preservation. Conversely, the labile tissues of organisms living in-situ in these up-slope communities are only rarely preserved due to the prevalence of more oxygenated conditions. Thus at different points along a water-depth transect these Tier II deposits are both supply- and decay-limited. Tier III deposits such as Latham or Indian Springs are hypothesized to have been deposited near storm wave-base in relatively oxygenated conditions, and soft tissues are almost completely decomposed. Or in another sense, only the most recalcitrant tissues are preserved (e.g., (23)). These Tier III sites are consequently the most ‘decay limited’ in this classification scheme.

This hypothesized relationship between BST preservation and the chemocline (10) has mainly been developed on the basis of sedimentological and ichnological data (e.g., (24)). To test this framework, in recent years geochemists have applied several tools to the question, most notably iron speciation analysis and the study of redox-sensitive trace metal concentrations. Both of these proxies rely on identifying enrichments of specific phases or elements (that are known to be incorporated into sediments under reducing conditions) relative to average crustal values or empirically determined shale baselines. Iron speciation tracks the ratio of total iron (FeT) to highly reactive iron phases (FeHR; iron in pyrite plus those iron phases reactive to sulfide on early diagenetic timescales, including iron oxides, iron carbonates and magnetite). In the modern ocean, samples deposited beneath an oxygenated water column have FeHR/FeT < 0.38 (25,26). Samples deposited beneath an anoxic water column generally have ratios > 0.38, although rapid deposition, for instance in turbidites, can mute enrichments (the lowest modern anoxic samples have ratios as low as 0.20; (25,27)). Critically, this proxy can also distinguish different types of anoxic water columns: between anoxic and ferruginous water columns (those with free ferrous iron, or more specifically not enough sulfide production to titrate available reactive iron) and anoxic and euxinic water columns (with free sulfide). This is accomplished by examining the proportion of reactive iron that has been pyritized (FeP; represents iron in pyrite). Generally, anoxic samples with FeP/FeHR > 0.7-0.8 are interpreted as euxinic, with ratios below this interpreted as ferruginous (26). As discussed below, whether a water column was ferruginous versus euxinic has important implications for interpreting trace metal patterns, and, perhaps, BST preservation itself.

Analysis of redox-sensitive trace metal concentrations relies on the observation that these elements (such as molybdenum, uranium, vanadium or chromium) are generally soluble in oxygenated water columns, and become insoluble and form complexes with organic matter, sulfides or other mineral phases upon reduction in suboxic (only trace amounts of oxygen present; ~ 0.1 mL/L) or anoxic (zero oxygen) water columns (28). Such authigenic metal enrichments are identifiable by comparing concentrations in a given shale sample against baselines meant to represent the background detrital input, such as world average shale (29) or average upper continental crust (30). Concentrations above these baselines would point towards authigenic enrichment, and by inference, a reducing water column. Like with iron speciation, rapid deposition will result in less time for authigenic enrichments to accumulate.

The sequestration pathways for each element are unique, with different reducing conditions and the presence/absence of sulfide having large effects on the level of enrichment. For instance, sulfide levels > 11μM are required for the quantitative switch from molybdate anion to tetrathiomolybdate, which increases particle reactivity and hence the removal of Mo from the water column into the sediment (31,32). Vanadium does not require sulfidic conditions for initial reduction, but also undergoes a second reduction step in the presence of significant sulfide levels (33), and the presence of large sedimentary V enrichments may require sulfide. Historically, most of the research on authigenic metal enrichment has focused on modern systems or Mesozoic Ocean Anoxic Events, both of which are characterized by water columns and sediments that were generally sulfidic when anoxic. However, ferruginous conditions are increasingly being identified throughout pre-Mesozoic oceans (26,34–36), and recent debate has focused on expected metal enrichments under such conditions (27,37–40). Although this debate remains open with respect to the exact magnitude of enrichment expected, studies have agreed that redox-sensitive metal enrichments will be relatively muted in ancient ferruginous settings. Further complicating the picture, two elements whose enrichment does not depend on the strict presence of sulfide—vanadium and chromium—are the redox-sensitive metals most influenced by variations in the detrital fraction, making the detection of muted enrichments difficult (28,41).

Redox studies of BST deposits

Analyses using iron speciation and some studies of redox-sensitive metal concentrations have provided contrasting interpretations of redox state during deposition of Burgess Shale-type deposits. Consistent with a role for anoxia in the preservational model, iron speciation analyses of the Series 3 Wheeler Shale, Utah, have indicated a mixture of ferruginous and oxic conditions ((35,42); although note that no data to date has been presented in stratigraphic or paleontological context). An iron speciation and trace metal abundance investigation of the Series 2 Chengjiang lagerstätte, South China, revealed euxinic conditions stratigraphically beneath the exceptionally preserved deposits, followed by the development of more 'equivocal' conditions in the zone of exceptional preservation (43). Specifically, Fe_P/Fe_{HR} ratios were <0.7, and Fe_{HR}/Fe_T ratios were between 0.2 and 0.38, which in combination with low Mo concentration and in the context of the turbiditic setting, could indicate either an oxic or ferruginous water column (43,44). Nitrogen isotopes were also investigated in these Chengjiang cores, and showed a more readily interpretable signal. Hammarlund et al. (43) suggested, based on positive nitrogen isotope values, that the water column was strongly denitrifying (similar to the cores of modern Oxygen Minimum Zones; OMZs) above the zone of exceptional preservation. Overall, these data point towards 'suboxic' to anoxic (but non-sulfidic) conditions during deposition of the Chengjiang BST deposits. Echoing these results, a detailed multi-proxy study of the Series 2 Sirius Passet deposit in North Greenland reported transiently anoxic (ferruginous) conditions during the interval of highest soft-bodied fossil abundance and diversity (45).

In contrast, trace metal data from these and other BST deposits have been interpreted as indicative of oxygenated conditions at the seafloor. Near-crustal levels of redox-sensitive metals (e.g. Mo, U, V, Cr) have been found in the Burgess Shale itself (46), Chengjiang (42,43; though higher abundances were found in the lower Maotianshan Shale), Sirius Passet (47), Emu Bay lagerstätte in South Australia (48), the Rockslide Formation in northwestern Canada (49), the Wheeler and Spence shales in Utah (44) and the Indian Springs lagerstätte, Nevada (50). These relatively low enrichments have generally been interpreted as representing a purely detrital trace metal source and an oxygenated water column. Consequently, it has also been inferred that anoxia did not play a role (or was not required) for BST preservation. In some cases, the robustness of these trace metal signals has been questioned because some deposits (such as the Burgess Shale and Sirius Passet) have experienced considerable metamorphism (24). However, given the consistent and widespread pattern in deposits with lower metamorphic grade, this is probably a primary depositional signature. But while likely primary, the common interpretative paradigm that low redox-sensitive trace metal contents indicate oxygenated conditions (e.g. Jones and Manning ref. (51)) was developed prior to our current understanding that anoxic but non-sulfidic (ferruginous) water columns—with low trace metal enrichments compared to euxinic systems—are common in the geological record. Given this new framework, these published trace metal data provide no evidence for euxinic conditions, but they are also consistent with the muted trace metal enrichments predicted for shale deposited under a ferruginous water column. Thus the role of redox state in BST preservation remains controversial.

The Mural Formation: a test case

The Lower Cambrian (Series 2) Mural Formation, exposed in the southern Canadian Cordillera (Fig. 1), offers an opportunity to refine our understanding of the role of redox state in BST preservation. In terms of preservation, the Mural Formation contains elements of BST soft-bodied preservation in one known locality near Mumm Peak (Fig. 1; Fig. 2D, E), but compared to Tier I and II biotas such as the Burgess Shale, Sirius Passet, Emu Bay, or Chengjiang, it is by no means 'exceptional' in terms of abundance or preservational fidelity. In essence, it preserves recalcitrant cuticles rather than fine morphologies. Also in contrast to most BST deposits that were deposited well beneath storm wave-base (10), the Mural Formation shows evidence of storm activity in stratigraphic proximity to the beds with exceptional preservation. The Mural Formation therefore represents an end-member of BST preservation: perhaps deposited in slightly shallower water, and with soft-part preservation not seen in standard shelly faunas, but not as exceptional as the deservedly more famous BST deposits. In the classification of Gaines (10) this is a 'Tier 3' BST deposit (the worst level of fossil preservation). The goal of this study is to conduct a multi-proxy sedimentary geochemical study of the BST-preservation interval in the Mural Formation—the first such study of a Tier 3 deposit—and compare the results against data obtained from other BST deposits worldwide. Overall this work provides data from a preservational end-member on the role of oxygen in BST taphonomy and an important consistency test of existing hypotheses: if anoxia plays a central role in exceptional BST preservation, we would predict a more oxygenated signal in the Mural Formation than the investigated Tier I and II deposits.

Geologic Background

The Mural Formation was deposited during the early Cambrian Sauk transgression on the western Laurentian margin (52,53), and sits above the ~300-1700 meter thick shallow-marine siliciclastics of the McNaughton Formation (54,55). The McNaughton is generally thought to represent the rift-to-post-rift transition on the Laurentian margin (56,57) although continued syn-sedimentary faulting continued through the mid-Cambrian to the north. The Mural Formation is part of a broadly contiguous stratigraphic package spanning the *Nevadella – Bonnia/Olenellus* trilobite zones (Series 2; Waucoban) that stretches from Mexico to Yukon, Canada (52). This package consists of an upper and lower carbonate composed of ooid grainstone shoals and archaeocyath bioherms, separated by a medial shale/siltstone (Fig. 3).

The Mural Formation has been the subject of paleontological investigation for more than a century (primarily at its type section near Mumm Peak, Jasper National Park, the focus of study here), and workers have described an abundant shelly fauna including trilobites and obollelid and linguliform brachiopods (58–63). Two known levels have also yielded soft-part preservation (Fig. 3), the '*Lingulosacculus* quarry' that preserves soft-shelled brachiopods (64) (Fig. 2E), and the 'waterfall quarry' level which contains as-yet undescribed vetulicolians, palaeoscolecid worms, and anomalocarid appendages (Fig. 2D). These soft-bodied preservation levels are located in grey, laminated shales between packages of shale containing beds and lenses of detrital carbonates, sometimes comprised of fossil hash. Whether these storm beds represent a shallowing into storm wave base during sea-level change (i.e. parasequences) or occasional storm beds at a constant depth could not be determined, but in either case this represents a proximity to wave base not seen in Type I and II BST deposits (10). The Mural Formation does not display bioturbation through the medial shale.

Materials and Methods

27 shale samples were collected from the Mural Formation, all from the medial shale at the type section, and crushed in a tungsten carbide shatterbox. Total organic carbon (TOC) weight percent was analyzed on decalcified residue on a Carlo-Erba NA 1500 Elemental Analyzer. Weight percent iron in pyrite (FeP) was quantified using the chromium reducible sulfur method of Canfield et al. (65), and iron present in iron oxides, iron carbonates and magnetite was quantified using the sequential extraction method of Poulton and Canfield (66). Precision estimates for these methods can be found in the supplementary materials of (35,40). Major, minor and trace element concentrations were analyzed by Bureau Veritas, Ltd., using ICP-MS/ICP-OES following multi-acid digestion. Aliquots of the USGS shale standards SBC-1 and SGR-1 were sent blind along with samples, and results were consistent with published values.

Results and discussion

All geochemical results are plotted on Figure 3 and reported in the Supplementary Information. Total organic carbon (TOC) weight percents in the Mural Formation are relatively low, at 0.14 $\pm$ 0.03 (one standard deviation). This probably rules out very high original sedimentary TOC values (as this signature can be retained even in the face of metamorphism, e.g., (67), but as these are outcrop samples from a region that has experienced prehnite-pumpellyite grade (CAI of 3-5) metamorphism (68), the original TOC-richness is unknown and certainly higher. Redox-sensitive trace metal contents are uniformly low and around crustal/average shale values. Specifically, Mo contents are all < 1 ppm, U contents are 2.6 $\pm$ 0.4 ppm, and V contents are 88 $\pm$ 8 ppm. As aluminum, a conservative tracer of detrital input, is also near or even slightly elevated compared to average shale values (9.4 ± 0.5 weight percent), the low redox-sensitive trace metal contents in the Mural cannot be explained by dilution by carbonates or other non-clastic material. Trace metal data are plotted in Figure 3 as Enrichment Factors (EF), which is a method of accounting for the expected detrital metal input based on observed levels of a biogeochemically conservative element such as aluminum (discussed in (28)). Values >>1 would indicate authigenic enrichment (due to reducing conditions). Values around 1 generally indicate the operation of purely detrital processes and oxic conditions, however since there is so much possible variability in detrital input (41), and substantial authigenic metal enrichments might also not develop during rapid sedimentation, recognizing whether there have actually been slight enrichments or depletions is difficult to tell. The Mural Formation data unfortunately falls in this zone. Thus, like many other BST deposits investigated to date, the Mural Formation trace metal data rule out euxinic conditions but are consistent with either an oxic (no enrichment) or ferruginous (possibly muted enrichment) water column during deposition.

The iron geochemistry of the Mural Formation, though, differs from that of investigated BST deposits. FeHR/FeT values are low (0.17 ± 0.04), with all of the values being well below the 0.38 ratio usually taken as indicative of an anoxic water column. The most straightforward explanation of these data is oxic deposition. However, it has been recognized that 1) fingerprinting anoxia is generally more straightforward than oxic conditions (37,69) and 2) there are a number of factors that can result in low FeHR enrichment (rapid deposition and source area effects) or drive FeHR/FeT values lower (metamorphism). Regarding rapid deposition, the medial shale does not have consistent sedimentological indicators of such processes, although it should be noted that obvious sedimentary structures are difficult to see in outcrop. There is evidence for event-driven sedimentation in a relatively thick sandstone marker bed right above the exceptionally preserved interval. Considering that almost all BST deposits involve event-based sedimentation (10), more detailed sedimentological and petrographic study of the Mural Formation may reveal additional evidence of these processes. Nonetheless, the observed FeHR/FeT values are still generally lower than the lowest 0.2 ratio recognized in the modern ocean for anoxic turbidites (27), suggesting a most parsimonious interpretation of oxic conditions even with respect to this caveat. Second, in some cases there may not be an appropriate source of detrital iron available to be shuttled into the anoxic basin, and it is this shuttle that ultimately generates the iron enrichments this proxy targets (discussed in (69)). However, such settings are relatively rare, and stratigraphically underlying anoxic Neoproterozoic strata exhibit obvious iron enrichments (36). Perhaps the most important consideration for the Mural is that highly reactive iron can be converted to poorly reactive iron during metamorphism, removing the evidence for anoxic sedimentation ((26,70). Fortunately, total iron (relative to aluminum) is also generally enriched by the iron shuttle under anoxic water columns (71,72), and this ratio is not as strongly affected by metamorphism. With the exception of one sample (interestingly, at the level of the *Lingulosacculus* quarry; Fig. 3), the Fe/Al values (0.48 ± 0.11) are exactly within the range expected of oxic sediments (72). In summary, although we cannot unambiguously rule out anoxic conditions, we can state 1) the only possible anoxic signal—in just one of multiple proxies—occurs at one of the soft-bodied preservation levels, and 2) all other available evidence points towards the presence of at least some oxygen in the water column (or more precisely, provides no evidence for anoxia).

The Mural Formation thus preserves elements of BST biotas and has no evidence for anoxia. Although seemingly paradoxical, we argue this provides strong evidence for the role of anoxic or periodically anoxic conditions in BST preservation. Put simply, the preservation in the Mural Formation is nowhere near that in the celebrated BST deposits. There is no exquisite, high-fidelity preservation of nervous systems, eyes, gut details, gills, etc. as in other deposits (73–76). The fossils preserved in the Mural Formation at Mumm Peak are the recalcitrant end-members of BST preservation: soft-shelled brachiopods (64), anomalocarid appendages, etc. Exceptionally preserved fossils in the Mural Formation are also rare and low-diversity; despite extensive quarrying during our fieldwork, we did not uncover new taxa that had not been found by previous field parties. Core

When comparing between BST deposits, it is worth noting that the overall differences in redox state may have been slight. For instance, the Mural is not extensively burrowed, suggesting the water column was not fully oxygenated. And some of the other more spectacular BST deposits may have been deposited in conditions that rapidly alternated between dysoxic and anoxic/ferruginous conditions, with the chemocline established perhaps only slight above the sediment-water interface (24). However, even considering the known difficulty of tracking low-oxygen conditions with available geochemical proxies (77), it is apparent that exceptional BST deposits (Tier 1 and 2) have a much greater prevalence of anoxic iron speciation signatures and/or total iron enrichments, minor but observable trace metal enrichments, and positive nitrogen isotope values (35,42,43,45) than the Mural Formation. In other words, there is now geochemical evidence suggesting both the Mural Formation and the transition between the upper Maotianshan Shale and Yuanshan Member 3 in the Chengjiang deposit (43) were more oxygenated and 'decay limited' than Tier I and II deposits. This confirms previous analyses based on detailed sedimentological and ichnological studies that preservation in BST deposits was facilitated by anoxic conditions (24).

Towards a refined geochemical model

Moving forward, it is clear that anoxia was likely involved in preserving BST fossils, but it is also clear from both sedimentological/ichnological approaches (24,78,79) and multi-proxy geochemical studies (43,45) that these deposits were near the edge of the chemocline, with often-times rapid fluctuations into low-oxygen (suboxic/dysoxic) conditions. Tracking low oxygen levels is difficult with our current geochemical toolkit (77), and further, the ecological/oceanographic timescales that matter for organismal habitat viability and fossil preservation often differ from the integrated longer-term geochemical signals studied in hand samples collected by geochemists (27). Indeed, no published multi-proxy BST dataset is completely unambiguous; such ambiguity may actually be a hallmark of very low-oxygen or fluctuating oxic/anoxic systems. In light of this, further gains in understanding of the role of redox conditions will require new approaches. These may include increased efforts to obtain unoxidized drill cores (packsack or 'winky' drills may offer an alternative to a full drill rig; e.g., (80)), and moving from standard bulk-rock geochemistry (such as in this study) to increased micron- and phase-specific interrogation of the geochemical signal, especially in more metamorphosed deposits. Shale-based proxies that can unambiguously resolve oxygenated conditions would also be a major step forward.

Most important, geochemical studies should strive towards a multi-proxy approach incorporating as many sources of data as possible, but especially pairing redox-sensitive trace metal analysis with iron speciation. The recognition that water columns were commonly ferruginous (non-euxinic) during this time interval will often make interpretation of trace metal data more difficult. Low Mo abundances are helpful in ruling out fully euxinic water columns

(81,82), but in the absence of iron speciation data (the best available method for fingerprinting anoxic but non-euxinic conditions), low concentrations of elements like U, V, and Cr are inconclusive as they could indicate either oxic or ferruginous conditions. Like the Mural Formation, some other ‘Tier 3’ lagerstätte such as Indian Springs might have been deposited under an oxic water column (50), but this cannot be determined from trace metal data alone. A further issue lies in choosing baseline values. Many studies compare redox-sensitive data to the interpretive scheme of Jones and Manning (51). This study was groundbreaking in its time (especially the cross-validation approach), but current consensus is that the scheme is optimistic in its true ability to detect such subtle redox shifts. Redox-sensitive trace metal behavior in sediments and the water column is complicated, and many of the Jones and Manning proxies (e.g. V/(V + Ni), Ni/Co or V/Cr) take two elements, each with incompletely understood redox properties and perhaps different detrital influences, and combine them together. The sum here is likely less than the parts. In light of this, we propose abandoning the Jones and Manning framework. Nuanced understanding of redox patterns with trace metals remains possible, but this should come through careful comparative study of metal data as single-element enrichment factors or metal/aluminum ratios (while paying heed to possible variation in detrital inputs (41)) and with respect to more modern chemical oceanographic studies.

How exactly anoxic (or fluctuating anoxic-to-dysoxic) conditions directly impacted BST preservation remains unclear. On the one hand, anoxia is a necessary but insufficient prerequisite for BST preservation by eliminating scavenging (10,19,21). Early calcium carbonate cementation and low oceanic sulfate levels may have been equally important in sealing beds from oxidant delivery and reducing microbial decay (83). Beyond simply considering ‘anoxia,’ it may actually be the specific flavors of anoxia in the sediment and water column that are important in controlling preservation. Specifically, 'suboxic' microbial processes such as iron and manganese reduction dramatically increase alkalinity relative to dissolved inorganic carbon (DIC) and thus raise the calcium carbonate saturation state of porewaters. In contrast, sulfate reduction increases alkalinity ~equal to DIC, and moves saturation state along lines of roughly equal values (Ω) (84). Enhanced iron reduction in Cambrian sediments could therefore have helped induce precipitation of the observed BST seafloor cements critical for 'sealing' carcasses in the sediment. It is worth noting here that many, but not all, of the BST cement layers carry a dominant seawater (rather than microbial) carbon isotope signature (83). However a seawater carbon signature can also be found in other carbonate precipitates believed to be triggered by 'suboxic' microbial metabolisms (84). Essentially, a dominantly seawater carbon isotope signature does not negate a role for iron reduction, but rather suggests that relatively little microbial respiratory work was required to tip the scales and induce precipitation (84).

The fact that there was abundant iron reduction relative to sulfate reduction during early diagenesis in BST deposits has recently been demonstrated by clay mineralogy studies. A recent investigation of 19 Cambrian sedimentary successions on four continents found that BST deposits were highly correlated with the presence of iron-rich clay minerals (berthierine and chamosite) compared to deposits only containing shelly fossils (85). These clays form during early diagenesis by the transformation of detrital clays in the presence of elevated pore-water Fe^{2+}. The exact role of these clays in preservation is unclear, specifically whether they are simply a symptom of some other factor important in BST preservational pathways, or a cause (86,87). Certainly, clays appear to function as anti-microbial agents in decay experiments (88), but the action of iron-rich clays is not significantly different from precursors like kaolinite, and the timescale for the formation of berthierine and chamosite is longer than the timescale required for labile tissue preservation. In any case, considering that pore-water Fe^{2+} will not accumulate in the presence of sulfide (89), it is significant that anoxic Cambrian water columns *and* sediments appear to have had relatively low sulfide-generating potential (35). Thus, a transition in the uppermost sediment column away from extensive iron reduction, and towards sulfate reduction (such as we see in modern OMZs) over the early Phanerozoic may have played multiple geochemical roles in the disappearance of BST preservation. In this view, a transition towards more oxygenated oceans with time may have been important (18), but this alone would be too simplistic; the relative rates of iron versus sulfate reduction matter too. In other words, as oxygen and sulfate levels rose through the Paleozoic (90,91), changes in sediments and water columns towards either more oxic or more sulfidic conditions may have inhibited BST preservational pathways. Most likely, the Burgess Shale-type taphonomic window was propped open by a ‘perfect storm’ of geochemical parameters in the Cambrian ocean (18,83,86,92).

Summary Points

- Poor preservation in Burgess Shale-type deposits is linked to relatively more oxygenated conditions, suggesting anoxia likely played a role in the most exceptionally preserved deposits.
- The relative dominance of iron reduction compared to sulfate reduction in Cambrian sediments and water columns may have played a key role in factors required for Burgess Shale-type preservation.

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Figure 1- A, B: Geographic position of the Mural Formation section studied here. C: Geological map of the study region, after GSC Map 1499A (93) and modified from (62).

Figure 2- Sedimentology and paleontology of the medial shale/siltstone of the Mural Formation near Mumm Peak. A: Unlike exquisitely preserved Tier I and II BST deposits, the medial shale contains beds and lenses of detrital carbonate with indications of wave or current activity, such as cross beds (arrow). Photo from 107.4 meters; mechanical pencil for scale. B) Shale beds immediately adjacent to beds with current structures have a shelly fauna, with evidence of transport, such as this cluster of trilobite cephalons. Photo from local float at 117 meters, mechanical pencil for scale. C) The lower half of the medial shale also contains laminated grey shale intervals, such as this photo spanning ~114-115 meters, at the 'waterfall quarry' level. 30 cm geological hammer for scale. These intervals host rare soft-bodied preservation. D) In-situ fragment of anomalocarid claw (arrow), from 114 meters (within 'waterfall quarry'); diameter of Canadian quarter is 24 mm. E) *Lingulosacculus nuda* (64) with preserved gut trace (arrow), from '*Lingulosacculus* quarry' at 118.2-118.6 meters. 5 mm scale bar on photo.

Figure 3- Lithostratigraphy and sedimentary geochemistry of the Mural Formation at Mumm Peak. Total measured thickness of the Formation is very similar to that of (59) but the heights of internal units differ slightly. *Nevadella-Bonnia/Olenellus* boundary is resolved to a 3.85m interval between 117.3m and 121.15m. Inset shows expanded stratigraphy of medial shale/siltstone. Geochemical data from left-to-right: 1) The iron speciation proxy (FeHR/FeT). Values above the vertical 0.38 line likely represent deposition under an anoxic water column, based on calibrations from the modern ocean (25). Oxic samples in the modern fall below this line, but anoxic samples can too, for instance during turbiditic sedimentation. The dashed 0.2 line represents the lowest modern value for an anoxic turbiditic sediment. FeP/FeHR values not graphed as all samples show an oxic signature; the average is 0.29 ± 0.15 (Supplemental Information) (27). 2) Fe/Al ratio, with shaded blue bar representing the range of values seen in ancient oxic shale (72). Values above this bar would indicate iron enrichment due to an anoxic water column. 3) Molybdenum Enrichment Factor (EF). 4) Uranium EF. 5) Vanadium EF. For these samples, an Enrichment Factor of 1 represents an aluminum-normalized value equal to upper continental crust (30). Values above 1 indicate enrichment, although recognition of muted enrichments can be difficult due to variations in detrital input (41). Enrichment would be expected under an anoxic water column (28), yet all of these samples are unenriched. McNton. = McNaughton Formation; W. = 'waterfall quarry' level from 112.8-114.9m; L. = '*Lingulosacculus* quarry' from 118.2-118.6m.

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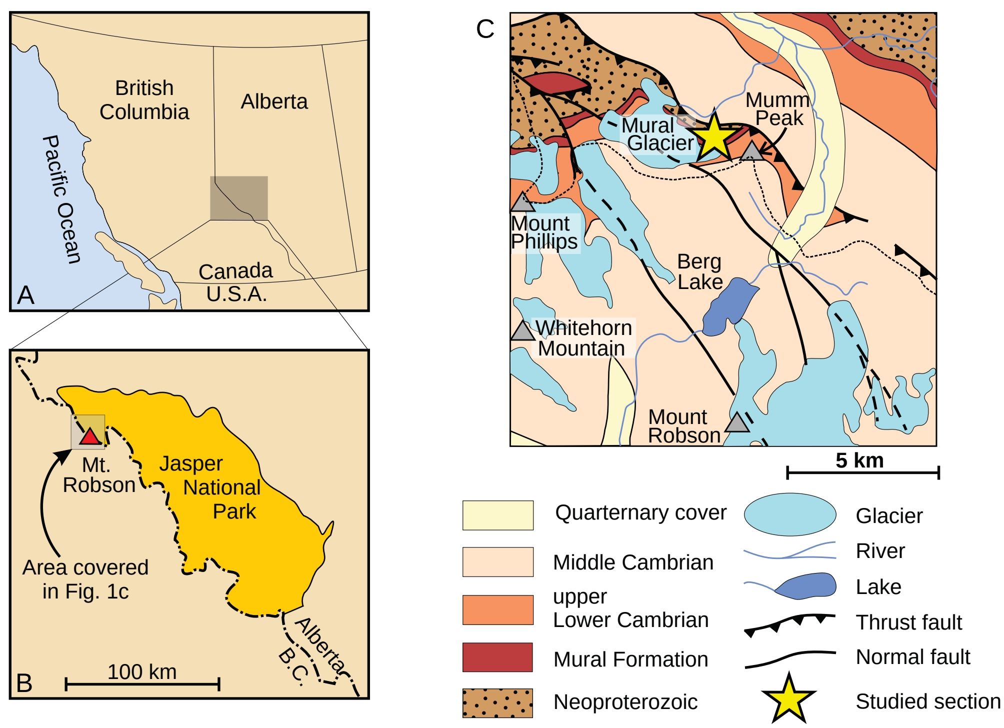
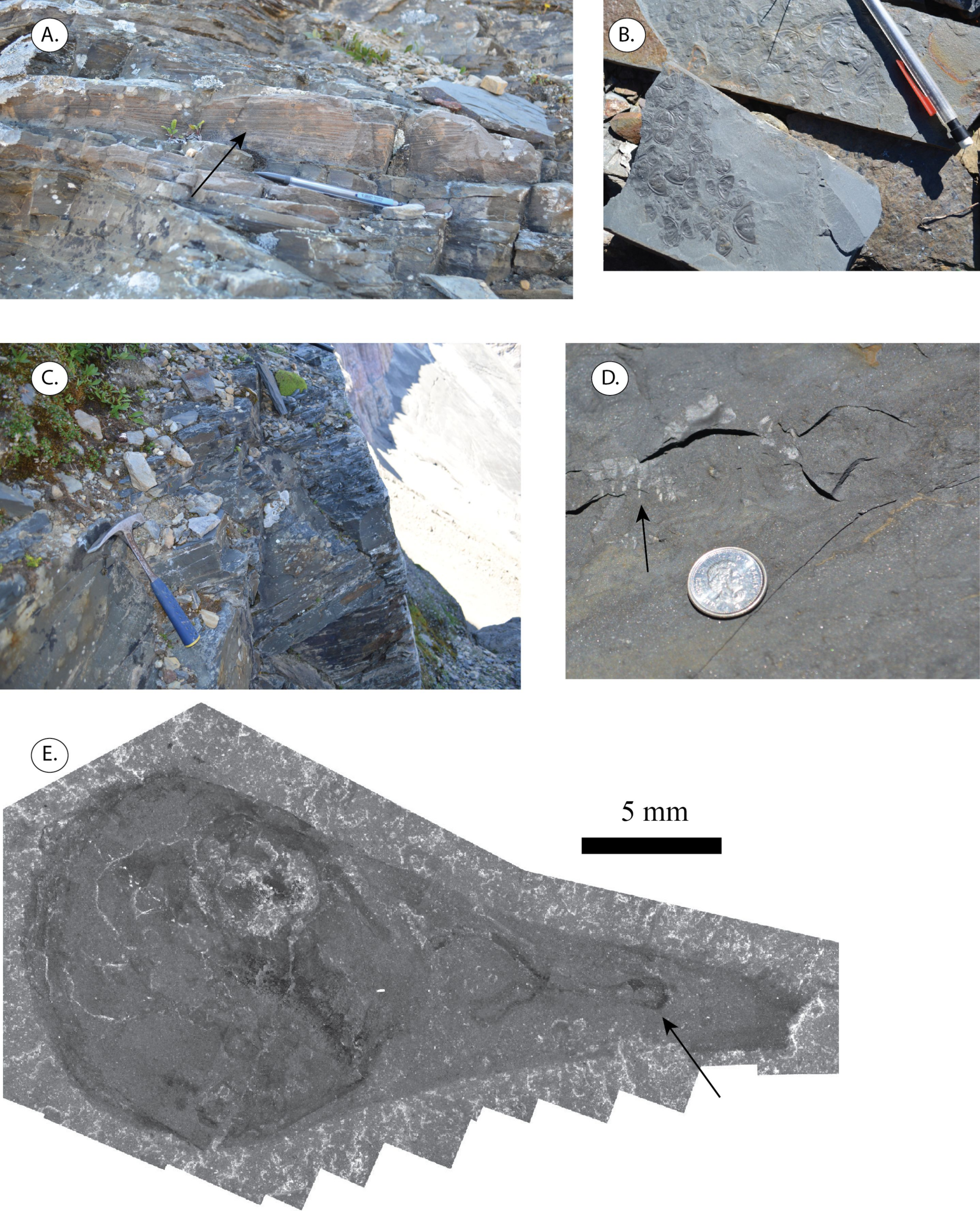
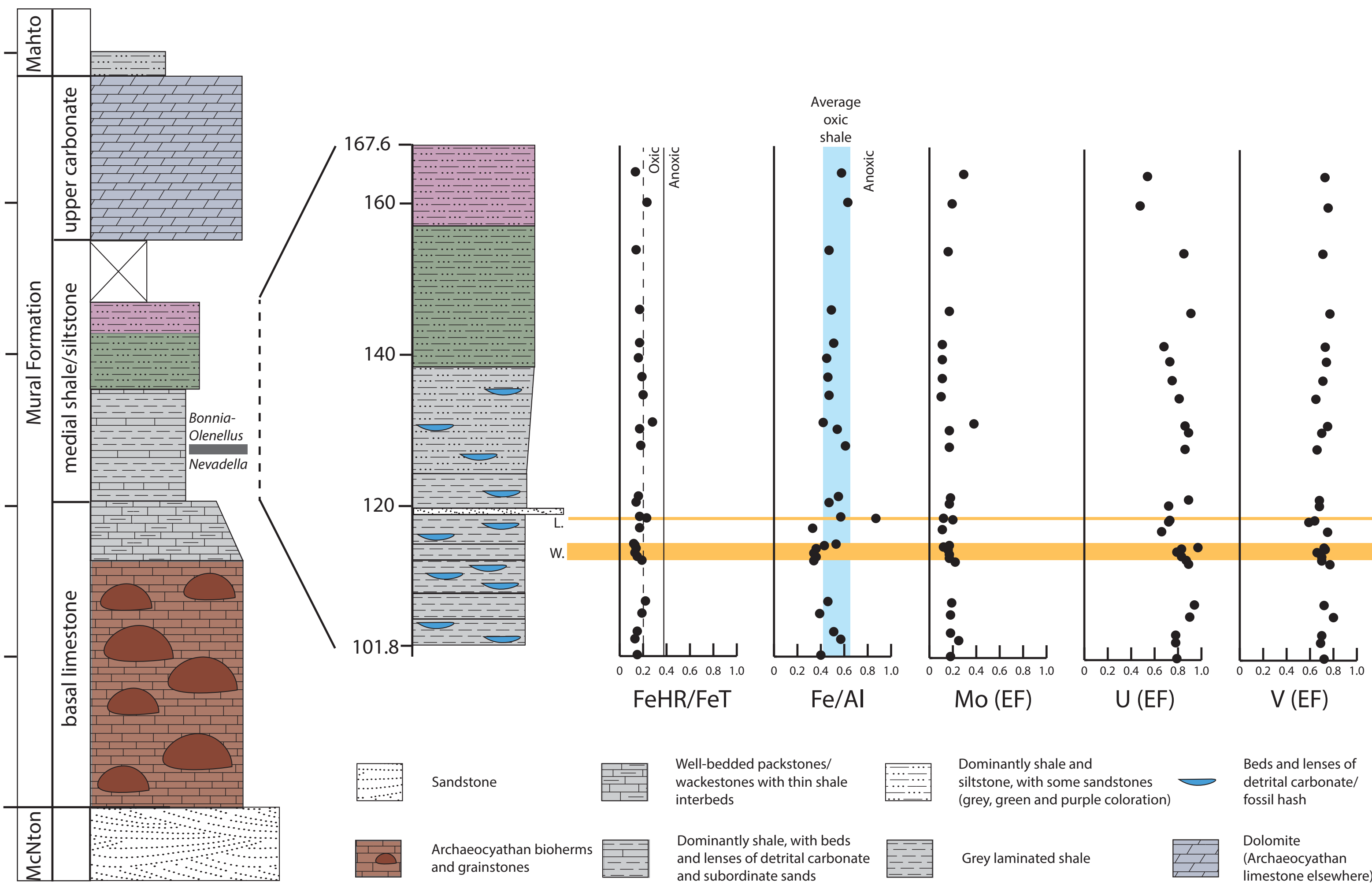

A
British Columbia
Alberta
Pacific Ocean
Canada
U.S.A.
B
Mt. Robson
Jasper National Park
Area covered in Fig. 1c
Alberta
B.C.
100 km
C
Mural Glacier
Mumm Peak
Mount Phillips
Berg Lake
Whitehorn Mountain
Mount Robson
5 km
Quarternary cover
Middle Cambrian
upper Lower Cambrian
Mural Formation
Neoproterozoic
Glacier
River
Lake
Thrust fault
Normal fault
Studied section


A.
B.
C.
D.
E.
5 mm



Mahto
Mural Formation
upper carbonate
medial shale/siltstone
basal limestone
McNton
250
200
150
100
50
0 m
Bonnia-Olenellus
Nevadella
167.6
160
140
120
101.8
L.
W.
Average oxic shale
Oxic
Anoxic
FeHR/FeT
Fe/Al
Mo (EF)
U (EF)
V (EF)
0 0.2 0.4 0.6 0.8 1.0
Sandstone
Archaeocyathan bioherms and grainstones
Well-bedded packstones/ wackestones with thin shale interbeds
Dominantly shale, with beds and lenses of detrital carbonate and subordinate sands
Dominantly shale and siltstone, with some sandstones (grey, green and purple coloration)
Grey laminated shale
Beds and lenses of detrital carbonate/ fossil hash
Dolomite (Archaeocyathan limestone elsewhere)

SGP sample_i	Original_num	Height_in_se	Lithology	Fe-carb (wt%	Fe-ox (wt%)	Fe-mag (wt%
3321	S1409-100.2	100.2	shale	0.188	0.176	0.122
3322	S1409-102.3	102.3	shale	0.267	0.144	0.145
3323	S1409-103.3	103.3	shale	0.177	0.218	0.186
3324	S1409-105.7	105.7	shale	0.127	0.225	0.097
3325	S1409-107.3	107.3	shale	0.148	0.421	0.165
3326	S1409-112.7	112.7	shale	0.138	0.218	0.098
3327	S1409-113.2	113.2	shale	0.112	0.108	0.123
3328	S1409-113.7	113.7	shale	0.113	0.053	0.151
3329	S1409-114.3	114.3	shale	0.108	0.097	0.173
3330	S1409-114.7	114.7	shale	0.144	0.085	0.18
3331	S1409-114.9	114.9	shale	0.161	0.073	0.179
3332	S1409-117	117	shale	0.102	0.115	0.077
3333	S1409-118.3	118.3	shale	0.241	0.476	0.375
3334	S1409-118.5	118.5	shale	0.21	0.161	0.298
3335	S1409-120.4	120.4	shale	0.166	0.042	0.187
3336	S1409-121.2	121.2	shale	0.248	0.058	0.195
3337	S1409-127.9	127.9	shale	0.499	0.078	0.27
3338	S1409-130.1	130.1	shale	0.339	0.08	0.218
3339	S1409-131	131	shale	0.214	0.174	0.15
3340	S1409-134.6	134.6	shale	0.245	0.095	0.186
3341	S1409-137	137	shale	0.183	0.041	0.156
3342	S1409-139.5	139.5	shale	0.238	0.054	0.224
3343	S1409-141.5	141.5	shale	0.313	0.06	0.277
3344	S1409-145.9	145.9	shale	0.125	0.344	0.237
3345	S1409-153.8	153.8	shale	0.14	0.097	0.16
3346	S1409-160.1	160.1	shale	0.143	0.964	0.218
3347	S1409-164	164	shale	0.117	0.461	0.129
			Average	0.19	0.19	0.18
			Standard Dev	0.09	0.20	0.07

Fe-py (wt%)	FeT (wt%)	FeHR	FeHR/FeT	Fe-py/FeHR	FeT/Al	TOC (wt%)
0.079	3.82	0.57	0.15	0.14	0.4	0.13
0.089	4.87	0.65	0.13	0.14	0.57	0.13
0.109	4.51	0.69	0.15	0.16	0.51	0.15
0.232	3.5	0.68	0.19	0.34	0.39	0.12
0.128	3.94	0.86	0.22	0.15	0.46	0.18
0.189	3.32	0.64	0.19	0.3	0.34	0.19
0.238	4.03	0.58	0.15	0.41	0.36	0.16
0.185	3.95	0.51	0.13	0.37	0.34	0.16
0.166	4.22	0.55	0.14	0.31	0.36	0.16
0.182	4.54	0.59	0.13	0.31	0.43	0.19
0.216	5.67	0.63	0.12	0.35	0.53	0.22
0.272	3.24	0.56	0.17	0.48	0.33	0.18
0.514	7.46	1.6	0.23	0.32	0.87	0.15
0.284	5.83	0.95	0.17	0.3	0.57	0.13
0.219	4.45	0.62	0.14	0.36	0.47	0.14
0.276	4.97	0.78	0.16	0.36	0.55	0.15
0.185	5.66	1.04	0.18	0.18	0.61	0.13
0.2	5.02	0.84	0.17	0.24	0.54	0.15
0.648	4.22	1.19	0.28	0.55	0.42	0.14
0.47	4.87	1	0.2	0.47	0.47	0.11
0.465	4.58	0.85	0.19	0.55	0.46	0.15
0.211	4.43	0.73	0.16	0.29	0.45	0.12
0.196	4.92	0.85	0.17	0.24	0.51	0.09
0.057	4.63	0.77	0.17	0.08	0.49	0.12
0.234	4.59	0.63	0.14	0.37	0.47	0.1
0.006	5.91	1.34	0.23	0.01	0.62	0.12
0.012	5.43	0.72	0.13	0.01	0.57	0.1
0.22	4.69	0.79	0.17	0.29	0.48	0.14
0.15	0.91	0.26	0.04	0.15	0.11	0.03

Al (wt%)	Ca (wt%)	K (wt%)	Mg (wt%)	Mn (ppm)	Mo (ppm)	Mo EF
9.08	1.27	4.37	1.36	245	0.3	0.18
8.48	4.11	3.8	1.38	629	0.4	0.25
8.85	0.77	4.18	1.36	246	0.3	0.18
8.96	0.09	4.92	0.97	82	0.3	0.18
8.52	0.11	4.16	1.05	105	0.3	0.19
9.64	0.09	5.42	0.81	104	0.4	0.22
9.21	0.07	4.91	1	167	0.3	0.17
9.71	0.14	4.67	1.05	195	0.3	0.17
9.84	0.26	4.66	1.12	255	0.3	0.16
9	0.34	5.13	1.12	265	0.2	0.12
9.2	0.09	4.59	1.21	241	0.3	0.17
9.96	0.07	5.68	0.82	106	0.2	0.11
8	0.47	2.57	1.86	703	0.3	0.2
8.99	0.44	3.42	1.48	479	0.2	0.12
9.51	0.27	4.39	1.09	276	0.3	0.17
9.03	0.4	4.1	1.2	539	0.3	0.18
9.33	0.72	3.92	1.45	1120	0.3	0.17
9.38	0.41	4.45	1.25	911	0.3	0.17
9.97	0.3	5.2	0.86	737	0.7	0.38
10.3	0.3	5.07	1.11	726	0.2	0.1
9.9	0.08	4.82	1.19	556	0.2	0.11
9.89	0.06	4.73	1.14	888	0.2	0.11
9.74	0.15	4.44	1.18	1256	0.2	0.11
9.42	0.08	3.94	0.98	588	0.3	0.17
9.83	0.04	4.23	1.02	266	0.3	0.16
9.55	0.08	2.62	1.16	1295	0.2	0.17
9.57	0.1	2.78	1.11	399	0.3	0.17
9.37	0.42	4.34	1.16	495.52	0.29	0.17
0.53	0.79	0.79	0.22	359.41	0.10	0.06

Na (wt%)	P (ppm)	Th (ppm)	Ti (wt%)	U (ppm)	U EF	V (ppm)
0.933	470	18.6	0.426	2.5	0.79	87
0.944	480	16.4	0.374	2.3	0.78	78
0.945	540	17.7	0.371	2.4	0.78	83
0.805	370	17.3	0.441	2.8	0.9	95
0.783	520	19	0.391	2.8	0.94	82
0.547	540	15.7	0.444	3	0.89	99
0.639	350	16.3	0.431	2.8	0.87	86
0.535	540	15.4	0.428	2.8	0.83	90
0.532	880	17.4	0.407	2.7	0.79	87
0.523	990	15.3	0.397	2.6	0.83	88
0.601	340	16.8	0.398	3.1	0.97	88
0.565	280	16.2	0.455	2.3	0.66	100
0.987	1430	15	0.309	2	0.72	63
0.89	1150	20.3	0.429	2.3	0.73	76
0.818	550	16.7	0.433	2.4	0.72	86
0.73	730	19.3	0.444	2.8	0.89	82
0.649	870	17.8	0.432	2.8	0.86	82
0.556	600	17.2	0.431	2.9	0.89	87
0.465	590	19.8	0.469	3	0.86	99
0.403	650	17.9	0.419	2.9	0.81	89
0.407	230	15.1	0.382	2.6	0.75	93
0.472	270	16.3	0.426	2.5	0.73	98
0.81	640	14.2	0.364	2.3	0.68	94
0.284	330	18.6	0.46	3	0.91	96
0.337	230	15	0.385	2.9	0.85	93
0.266	300	12.4	0.362	1.6	0.48	94
0.277	260	13.1	0.376	1.8	0.54	92
0.62	560.37	16.70	0.41	2.59	0.79	88.41
0.22	295.55	1.94	0.04	0.38	0.11	8.21

V EF	Zn (ppm)	Zr (ppm)
0.72	51	74.7
0.69	60	70.1
0.7	62	68.1
0.8	54	73
0.72	56	81.5
0.77	41	80.2
0.7	58	68.6
0.7	66	68.8
0.66	71	61.1
0.73	70	59.9
0.72	103	59.7
0.75	37	69.8
0.59	124	45.5
0.64	92	60.3
0.68	61	59.9
0.68	80	63.4
0.66	109	55.9
0.7	100	57
0.75	61	70.4
0.65	83	61.8
0.71	93	64.1
0.74	88	72.2
0.73	96	67.9
0.77	73	78.5
0.71	76	75.2
0.74	78	36.3
0.72	68	38.5
0.71	74.48	64.53
0.04	21.04	11.27