Cambrian Burgess Shale Animals Replicated in Clay Minerals

Patrick J. Orr,* Derek E. G. Briggs, Stuart L. Kearns

Although the evolutionary importance of the Burgess Shale is universally acknowledged, there is disagreement on the mode of preservation of the fossils after burial. Elemental mapping demonstrates that the relative abundance of elements varies between different anatomical features of the specimens. These differences reflect the compositions of the minerals that replicated the decaying organism, which were controlled by contrasts in tissue chemistry. Delicate morphological details are replicated in the elemental maps, showing that authigenic mineralization was fundamental to preserving these fossils, even though some organic remains are also present.

The increase in metazoan diversity during the Cambrian period is one of the most important events in the history of life. The nature, extent, and timing of this radiation continue to be debated (*1*). Evidence of the nature of the organisms that evolved during the Cambrian is preserved in the Burgess Shale (Stephen Formation: Middle Cambrian) of British Columbia, Canada (*2*), and similar fossil deposits (*3*). In the Burgess Shale, the soft tissues of organisms are preserved as well as the biomineralized skeletons that are normally present, resulting in a more complete picture of diversity in the Cambrian seas (*4*).

Understanding the mode of preservation is a prerequisite for an interpretation of the morphology of soft-bodied fossils, especially those for which there are no obvious extant analogs. The Burgess Shale organisms are generally considered to have been incorporated into a series of event beds, representing turbidites deposited in relatively deep water at the foot of the Cathedral Escarpment (*4*, *5*). In spite of their importance to our understanding of early metazoan evolution, however, the mode of preservation of Burgess Shale–type fossils has remained unresolved.

There are two main and opposing models. Butterfield (*6*, *7*) showed that parts of some Burgess Shale taxa could be isolated as films of organic carbon, and he interpreted the preservation of the fossils as a result of decay inhibition and the preservation of organic material. The reflectivity of the fossils under incident light was enhanced by the alteration of the carbon to kerogen or graphite. The decay resistance and subsequent preservation of the organisms were attributed to incapacitation of microbial autolytic and digestive enzymes and the stabilization of structural polymers, as a result of interaction with clay minerals. These clay minerals, introduced at the time of deposition, enveloped the organism and were "forcibly injected" [p. 279 in (*6*)] into the body cavity. Previous reports that the fossils were composed of aluminosilicates of diagenetic origin (*4*, *8*) were explained as a result of sediment exposed within the outline of the fossil during splitting of the specimen.

In the alternative model (*9*), Towe argued that, although some Burgess Shale specimens yield organic remains, this does not account for all the features of the fossils: The presence of carbon is incidental to the preservation of morphological details. He considered that the organisms were buried in a thixotropic sediment that was injected into body cavities. The outlines were replicated as a result of gel stabilization; compression and cementation followed. The reflectivity is enhanced by the compression and orientation of clay minerals against the fossil.

Elemental mapping can be used to interpret the anatomy and taphonomy of exceptionally preserved fossils. This technique allows the relative abundance of elements in different parts of the Burgess Shale fossils and the adjacent matrix to be determined (*10*) (Fig. 1). The matrix adjacent to the specimens exhibits relatively constant concentrations of each element; thus, parts of the fossil can be regarded as elevated or depleted relative to the surrounding sediment. The results indicate that neither of the above-mentioned models can completely explain the preservation of Burgess Shale fossils.

Specimens of *Marrella* are characterized by elevated concentrations of Si (Fig. 1A). The stomach is distinguished by elevated Al, K, and C (Fig. 1A). Similar concentrations of these elements in the cephalic canals confirm that they were connected to the stomach (*11*) and suggest that they were composed of similar tissues. These canals presumably functioned in digestion. The line of the rest of the gut along the axis of the trunk, in contrast, has elevated Si and depleted Al and K (Fig. 1B). This is also the case for the "dark stain," a familiar feature of specimens of *Marrella* (*5*), which is interpreted as the result of leakage from the decaying organism (Fig. 1A). The lateral margins of the trunk display serially repeated structures, corresponding in position to the body somites, where Al and K are elevated and Si and, less notably, Ti and Fe are depleted (Fig. 1B). These areas coalesce to form a line flanking each side of the position of the gut. They may represent the shrunken remains of segmental muscles (*12*).

The specimen of *Alalcomenaeus* (Fig. 1C) shows elevated concentrations of Si and depleted concentrations of Ti, Al, and K, relative to the matrix. Four (two partially overlapping pairs) of the five eyes are evident and are picked out by prominent elevations of Al and K. Variations in the concentrations of Si, Al, and K along the body axis correspond to the overlapping boundaries of the cephalic shield and the anterior thoracic tergites. The gut trace has depleted Si and elevated Al and K. Its infill is dominantly phosphatic, showing high concentrations of Ca and P. A narrow band of elevated Al and K peripheral to the infill may correspond to the gut wall.

Elemental mapping confirms the presence of organic C in the fossils. Associated with the C, however, are minerals, dominantly hydrous aluminosilicates (*13*), which are presumably the products of diagenesis and metamorphism (*14*, *15*) of clay minerals. Where Fe and S are associated, the mineral is pyrite.

There is correspondence between the distribution of elements and anatomical features of the arthropods (and the dark stain in *Marrella*); there are differences in the relative abundance of the elements between the fossils and the adjacent matrix. The aluminosilicates that define the fossil therefore cannot be a product of sediment introduced during, or shortly after, burial, as envisaged in previous models for the preservation of the Burgess Shale fossils (*6*, *7*, *9*). Voids created during decay would have been occluded by collapse (*16*) and subsequent compaction, preventing infilling by late diagenetic minerals. Thus, where aluminosilicates occur within the fossils [Fig. 4 in (*6*)], they must have been introduced after entombment but before the collapse and compaction of the organisms; they are therefore of early diagenetic origin.

The differences in the compositions of the clay minerals in different parts of the fossils must have been controlled by contrasts in the chemistry of the decaying tissues (*17*). The elemental composition of the tissues may have controlled binding or precipitation of the minerals directly. Alternatively, the control may have been indirect, the more reactive clay minerals or cations preferentially occur-

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Department of Earth Sciences, University of Bristol, Queen's Road, Bristol BS8 1RJ, UK.

*Present address: Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, UK.

ring on more labile tissues. The sequence of mineralization would then reflect a progression from labile to more decay-resistant parts of the organism.

The affinity between clay minerals and organic matter (*18*) provides a mechanism for replicating decaying tissue. Colloidal or particulate clay minerals may have accumulated on this template; alternatively, clay minerals could have precipitated directly onto the tissues where suitable cations were present in solution in the pore waters. Such a mode of preservation was used to explain the replacement of muscles by authigenic clays in the giant Ordovician conodont *Promissum pul-*

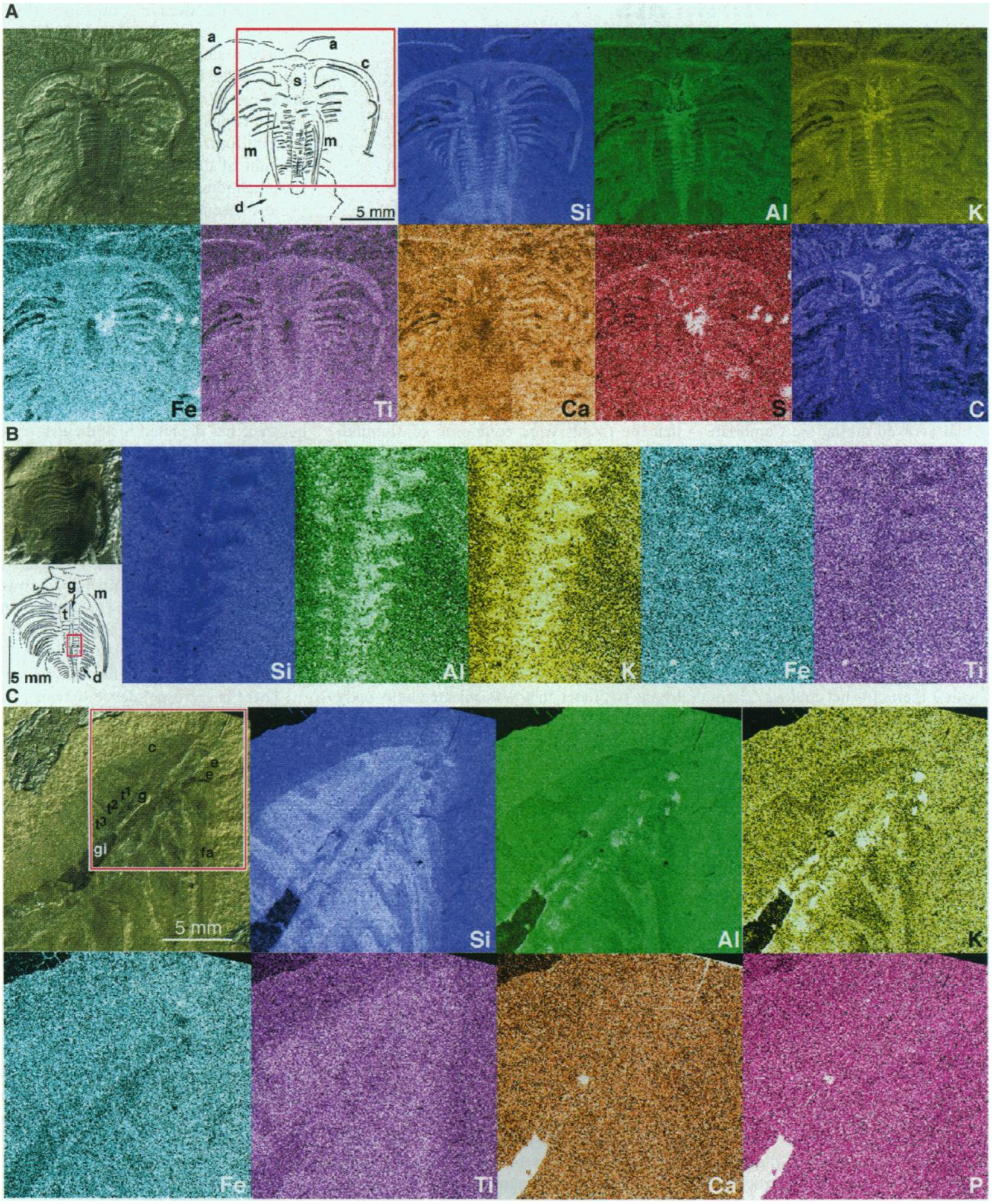

Fig. 1. Elemental maps for areas indicated on specimens of (**A** and **B**) *Marrella splendens* Walcott, 1912, and (**C**) *Alalcomenaeus cambricus* Simonetta, 1970. Each map displays the relative abundance of the element in terms of contrasts in tone; the brighter the tone, the more abundant the element. Abbreviations in(A) and (B): a, first antenna; c, lateral cephalic spine; d, dark stain; g, gut; m, median cephalic spine; s, stomach; t, trunk. Abbreviations in (C): c, cephalic shield; e, eyes; fa, frontal appendage; g, gut trace; gi, gut infill; t^1, t^2, and t^3, thoracic tergites. Specimen details: (A) University of Bristol 13352, (B) Royal Ontario Museum, Canada 53348, and (C) Museum of Comparative Zoology, Harvard 5969.

chrum and other taxa from the Soom Shale of South Africa (*19*). Kaolinite has been reported within the shells of Carboniferous lingulid brachiopods, where it contrasts with the illitic/smectitic composition of the adjacent matrix; the degradation of acidic glycosaminoglycans generated intraskeletal voids and mediated precipitation of clay minerals within them (*20*). Bacteria and other microorganisms can bind metals at their surface that, in turn, act as the nucleation sites for the growth of authigenic minerals, including Fe- and Al-rich silicates (*21*, *22*). The anionic cell surfaces of bacteria that form biofilms may enhance the fossilization potential of decaying leaves by binding cations such as Fe^{3+} (*23*). Detrital minerals can also be adsorbed on the surface of bacterial cells (*21*). Fossilized bacteria have not been identified in association with Burgess Shale fossils, but this does not eliminate a role for microorganisms in the preservation process. They may not have been preserved, or they may have been obliterated during later diagenesis (*15*).

The organic-walled structures recovered from the Burgess Shale include the sclerites of *Wiwaxia* (*6*), the setae of *Canadia* (*6*), and the "thick-walled" [p. 111 in (*7*)] cuticle of *Ottoia* and gut of *Eldonia*. There is no doubt that decay resistance played an important role in the fossilization of these structures. However, the evidence presented here shows that replication by minerals accounts for the detailed preservation of the more labile tissues that makes the Burgess Shale fossils so remarkable.

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Variation of Interplate Fault Zone Properties with Depth in the Japan Subduction Zone

Susan L. Bilek* and Thorne Lay

The depth dependence of physical properties along the Japan subduction zone interface was explored using teleseismic recordings of earthquake signals. Broadband body waves were inverted to determine the duration of rupture and source depth for 40 interplate thrust earthquakes located offshore of Honshu between 1989 and 1995. After scaling for differences in seismic moment, there is a systematic decrease in rupture duration with increasing depth along the subducting plate interface. This indicates increases in rupture velocity or stress drop with depth, likely related to variation in rigidity of sediments on the megathrust.

Subduction zone earthquakes exhibit spatial variability in rupture processes, including maximum magnitude, subevent complexity, and recurrence rate. Most studies have emphasized along-strike variations in rupture behavior, seeking explanations in terms of plate roughness, age, or convergence rate (*1*). Some studies have addressed spatial variability with depth, emphasizing thermal controls on the seismogenic interplate contact (*2*). Unusual tsunamigenic events that occur at shallow depth have been found to have anomalously long rupture durations, possibly because they occur in low-rigidity sediments (*3*). It is desirable to determine whether rupture properties vary with depth and to relate these variations to expected processes in the fault zone, such as dehydration and cementation of sediments, offscraping of sediments, increasing pressure and temperature conditions, variations in permeability, or phase transitions.

To probe variations in physical properties that may be manifested in earthquake behavior along the subduction zone interface, we used the duration of seismic energy release during faulting as a proxy for rigidity. Rupture duration is dependent on rupture velocity, which is generally found to scale with shear wave velocity v_s (*4*, *5*). Rupture duration also depends on the rupture area and the mode of rupture, so it is necessary to scale results for events with

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Institute of Tectonics and Earth Sciences Department, University of California, Santa Cruz, CA 95064, USA.

*To whom correspondence should be addressed. E-mail: sbilek@es.ucsc.edu