A perfect (geochemical) storm yielded exceptional fossils in the early ocean

Timothy W. Lyons¹

Department of Earth Sciences, University of California, Riverside, CA 92521

he geologic record treats us to rare examples of dazzling preservation of fossil animal remains. None is more spectacular than the faithful traces of even the most delicate soft tissues that are best and most commonly expressed during the early and middle parts of the Cambrian Period approximately 540 to 500 Mya and epitomized by the famous Burgess Shale in British Columbia (Fig. 1). Models for the mechanisms behind such extraordinary soft-tissue fossilization abound. The problem, though, is that most invoke conditions, such as rapid deposition beneath oxygen-poor seawater, that are far more common through time than the special fossils themselves. Now, Gaines et al. (1) tackle this conundrum by taking a decidedly nonuniformitarian view of the global Cambrian ocean-asserting that chemical conditions came together to vield an unusual if not unique preservational window.

We have all seen a rotting jellyfish on the beach or festering road kill along the highway. Bacteria are fast-acting and ubiquitous, and so the preservation of soft tissue-fossil remains other than hard bones or shells such as guts and gills-requires something out of the ordinary. Rapid entombment on the seafloor helps, as by the large amounts of mud kicked up by storms and underwater avalanches known as turbidites, which bury the rotting remains away from the bacteria-favoring oxygen in the overlying seawater. An ocean poor in dissolved O_2 in the deeper waters would help, and such conditions may have abounded during the Cambrian (2).

From a platform of past experience and new data, however, Gaines et al. (1) remind us that even rapid burial under oxygen-free waters is not enough to explain the extraordinary preservation of "Burgess Shale-type" fossils. They specifically refined their perspectives on fossil preservation through detailed geochemical and sedimentological analysis of many of the world's spectacular Burgess Shale-type fossils and their host rocks, including the Burgess Shale proper, which C. D. Walcott of the Smithsonian Institution discovered a century ago. Also included in the analytical mix is new drill core from the Chengjiang interval of the Early Cambrian Yu'anshan Formation near Haikou, Yunnan, China. Fresh, un-



Fig. 1. Arthropod fossil from the Burgess Shale described by C. D. Walcott in 1912 as *Sidneyia inexpectans* (named in honor of his son, Sidney). The beautiful traces of soft tissue preserved as carbonaneous films include the feathery gill structures seen readily in the photograph. The Burgess Shale, the most famous of the Cambrian fossil deposits, is marked by exceptional preservation of soft tissue, including remarkable records of soft-bodied organisms lacking skeletal remains. (Image is in the public domain; from ref. 9.)

weathered core material is particularly well suited to geochemical analysis.

Their perspective on ancient organic decay builds, as it must, on a generation of pioneering research in the laboratory and modern ocean. These lessons have taught us that the currency in the energyyielding processes of bacterial metabolisms lies with the electrons transferred during oxidation of organic remains (i.e., electron loss), and O_2 is the most energetically favorable electron acceptor and thus facilitator in the rapid loss of soft tissue (3). However, sulfate (SO_4^{2-}) is also abundant in modern seawater, second only to Cl⁻ among the anions, and many bacteria can efficiently oxidize (i.e., degrade) organic remains by reducing sulfate to hydrogen sulfide (H₂S) in the process. In fact, in many coastal settings in the modern ocean, as much organic decay happens through bacterial sulfate reduction as through aerobic (i.e., O₂-related) processes (4). In a competitive sense, aerobic decay is more energetically favorable, but burial within the sediments isolates the decaying organic matter from the overlying source of O_2 . The big difference between the two pathways is that abundant bacterial sulfate reduction only occurs anaerobically, in the absence of oxygen. We are left with the distinct possibility that soft tissue could have been consumed quickly even when faced with rapid burial beneath an O2-lean Cambrian oceanunless sulfate was scarce in that early seawater.

Perhaps the most important insight proffered by Gaines et al. (1) lies with the suggestion that the exceptional Burgess Shale-type preservation is indeed a manifestation of low sulfate concentrations in the Cambrian ocean. Seawater sulfate concentrations at only a small fraction of today's are a common theme in studies of the Precambrian ocean more than 540 Mya, reflecting a sequence of bacterial sulfate reduction and subsequent formation of pyrite (FeS₂) when the resultant hydrogen sulfide reacted with iron (reviewed in ref. 5). Pyrite burial is ultimately a sink for sulfate and prospers when large portions of the deep ocean are O₂-free, as has been suggested for most, if not all, of the Precambrian (6). Today, such conditions are limited to small areas of the ocean (much less than 1%), with the Black Sea being our best example. However, recent work is pointing to a reprise of the widespread anoxia of the Precambrian during the Cambrian (2), and low concentrations of seawater sulfate may have been the result.

Gaines et al. (1) support this assertion of low sulfate availability with independent

Author contributions: T.W.L. wrote the paper.

The author declares no conflict of interest.

See companion article on page 5180.

¹E-mail: timothy.lyons@ucr.edu.

evidence that lies with the sulfur isotope composition of pyrite at the Chengjiang locality in China. Bacteria not only reduce sulfate to hydrogen sulfide, but they do so with a strong preference for the light sulfur isotope, ³²S, compared with the heavier ³⁴S. Enrichments in ³²S in the resulting pyrite are a telltale sign of bacterial sulfate reduction under sulfate-replete conditions. When sulfate becomes limiting, however, something very different happens: the bacteria lose much, if not all, of their ability to distinguish between ³²S and ³⁴S when reducing sulfate—in the extreme case when they reduce it all. Pyrite with ³⁴S/³²S ratios approaching those of the starting sulfate of the global ocean suggests that sulfate was in limited supply, and this is just what Gaines et al. observe in China (1).

There is one more chapter in this story. Sulfate, even when present in small amounts in the ocean, can diffuse from seawater into the sediments, sustaining anaerobic decay of soft tissue and fractionating sulfur isotopes in the process. This possibility also occurrs to Gaines et al. (1). The final step, then, demands a control that might have limited the diffusional flow of sulfate from the seawater into the pore fluids within the sediments that covered the seafloor. One possibility for restricting flow is very early and rapid cementation of those sediments by calcium carbonate precipitated from an ocean with a high state of saturation with respect to carbonate minerals such as calcite and aragonite. Past studies of the Cambrian ocean have suggested unusually high alkalinity that may have favored rapid and pervasive formation of early calcium carbonate cements on or just below the seafloor (e.g., ref. 7), and Gaines et al. (1) bring their own evidence for this condition to the table. The random orientations of tabular, microscopic clay minerals that they observed in Burgess Shale-type fossil

- Gaines RR, et al. (2012) Mechanism of Burgess Shaletype preservation. Proc Natl Acad Sci USA 109:5180– 5184.
- Gill BC, et al. (2011) Geochemical evidence for widespread euxinia in the later Cambrian ocean. *Nature* 469:80–83.
- Froelich PN, et al. (1979) Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: Suboxic diagenesis. *Geochim Cosmochim Acta* 43: 1075–1090.

beds point to rapid deposition and, quite likely, early cementation. (Compaction during burial can otherwise flatten out the random, "house-of-cards" structures with which clays typically start.) Also, reworked slump deposits that formed penecontemporaneously with sediment deposition show signs of very early, preslump cements, and their arguments are consistent with carbon isotope data that suggest a seawater source for most of the cement.

At the end of the day, Gaines et al. posit a perfect storm of taphonomic conditions.

The surface cement could have provided a cap that inhibited further transport of sulfate into the sediment layers below and thus restricted further anaerobic decay of the associated organic remains, which were buried rapidly beneath an $O_{2^{-}}$ and sulfate-lean ocean.

Gaines et al. (1) are not the first to express their opinions on the special conditions required to preserved carbonaceous traces of soft tissue in Burgess Shale-type fossils. Indeed, these fossils and their special preservation are among the most talked-about themes in studies of taphonomy-the science that deals with the postmortem transformation of decaying remains in soft mud to fossils preserved in rocks over many millions of years. However, by looking for common themes among the deposits, generating new geochemical data, and tying the observations to the best estimates of chemistry in the Cambrian ocean, they provide unique insight—in particular, the purported relationships to hypothesized low sulfate conditions and high levels of calcium carbonate saturation. These

- Jørgensen BB (1982) Mineralization of organic matter in the sea bed — the role of sulphate reduction. *Nature* 296:643–645.
- Lyons TW, Gill BC (2010) Ancient sulfur cycling and oxygenation of the early biosphere. *Elements* 6: 93–99.
- 6. Canfield DE (1998) A new model for Proterozoic ocean chemistry. *Nature* 396:450–453.
- Brennan ST, Lowenstein TK, Horita J (2004) Seawater chemistry and the advent of biocalcification. *Geology* 32:473–476.

factors, they argue, led collectively to low amounts of anaerobic decay (i.e., in absence of O_2).

At the end of the day, Gaines et al. (1) posit a perfect storm of taphonomic conditions expressed perhaps universally among the many globally distributed localities of Burgess Shale-type fossil preservation of approximately the same age: low sulfate in the ocean along with high carbonate saturation states that favored almost immediate cementation of sediments deposited rapidly beneath an oxygen-poor ocean. Rapid deposition and widespread ocean anoxia are common features over the history of animal life, yet spectacular fossils are typically not the result. In the minds of Gaines et al., the "just-right" chemical conditions in the ocean delivered the silver bullet.

We might be inclined to argue that such serendipity is too much to hope for, but the response would be that extraordinary fossils are extraordinarily rare and never the children of typical conditions. We might also argue that the necessary ocean chemistry requires further study. For example, could carbonate cementation really have been fast and pervasive enough to stifle decay so effectively? How low was sulfate in the Cambrian ocean, and was it low enough to inhibit decay (8)? Regardless, Gaines et al. (1) give us key observations and geochemical data and build on a foundation laid from a large body of past work, including their own, that all point to the possibility of a perfect storm.

It is our good fortune that ocean evolution may have given us a very special physio-biogeochemical window to view the early diversification of animal life across the globe—but perhaps it did so uniquely and narrowly in time over the approximately half billion years of animal history.

- Hammarlund E, et al. (2011) The Influence of Sulfate Concentration on Soft-Tissue Decay and Preservation. Palaeontographica Canadiana (Geological Association of Canada, St. John's, NL, Canada), Vol 31, pp 141–156.
- Walcott CD (1912) Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. Smithson Misc Collect 57(6):148–228.