Flume experiments reveal flows in the Burgess Shale can sample and transport organisms across substantial distances

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The exceptionally preserved fossils entombed in the deposits of sediment-gravity flows in the Cambrian Burgess Shale of British Columbia have been fundamental for understanding the origin of major animal groups during the Cambrian explosion. More recently, they have been used to investigate the evolution of community structure; however, this assumes that the fossil assemblage represents an in-life community. Here we test this assumption for the first time based on experimental and field approaches. We use flume experiments to create analog flows and show that transport of the polychaete *Alitta virens* over tens of kilometers does not induce significantly more damage beyond that already experienced due to normal decay processes. Integration of experimental results with taphonomic assessment of fossils and sedimentological analysis suggests that the organisms of the Burgess Shale in the classic Walcott Quarry locality could have undergone substantial transport and may represent a conflation of more than one community.

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The fossil record provides an archive of the diversity of life through time and has been used to identify major developments of diversification and extinction. Whilst it is known that this archive is incomplete at the global scale, methods may be applied to global diversity curves to correct for variation in sampling intensity with geological age¹. At the community level, most individual fossil assemblages comprise organisms with biomineralized hard-parts; the exception being fossil Konservat Lagerstätten that, in addition, preserve soft-tissues and soft-bodied organisms. It is predicted that 30% of modern marine megafauna² and 80% of macrofauna genera³ would leave no fossil record, whilst 86% of genera from the Burgess Shale would not have been preserved under normal circumstances⁴. This has led to Burgess Shale-type lagerstätten being viewed as near-faithful representations of in-life communities and, as such, they have been used to reconstruct Cambrian marine community structure^{4–6} and food-webs⁷. Determining whether these lagerstätten record community structure with high fidelity or if they are biased representations is critical to our ability to describe palaeocommunities, compare ecosystem complexity through time, and study evolutionary patterns to understand how life has evolved to its present diversity.

Fossilization of soft tissue is rare. Decay experiments with analog organisms have yielded a wealth of information in this area, revealing the significant effects of decay processes of mineralization of soft tissues and how it results in the systematic alteration and loss of phylogenetically informative features^{8–12}. However, studies concerning the effect of transport on the preservation of organisms are surprisingly limited and have tended not to consider analog sediment transport mechanisms that may be used to test and constrain the effects of sedimentary processes on the fossil record^{8,13}.

The Burgess Shale Lagerstätte is one of the most important paleontological discoveries of the last century. Soft-tissue preservation of these animals offers insights into the biodiversity of the Cambrian marine realm and, together with over 40 localities worldwide that exhibit “Burgess Shale-type preservation” reveals a marked phase of diversification of body plans in the aftermath of the Cambrian explosion^{14–18}. There is debate regarding the extent of transport that the organisms of the Burgess Shale experienced in its type locality. This has hinged on consideration of either the types of deposits and flows responsible^{4,19,20} or the quality of preservation²¹, but we advocate that these must be considered together. Originally, the deposits were argued to be

Fig. 1 Increasing states of polychaete degradation. *Alitta virens* (right) and comparable states in the fossil, *Burgessochaeta* (left). **A** State 1-complete polychaete, entire body segment intact (ROM-64913). **B** State 2-damage towards the mid-section and posterior transforms into tangled remains caused by the combination of transport and decay. The body remains intact as one segment (ROM-64916). **C** State 3-remains of the trunk and setae. The body structure has deteriorated significantly (ROM-64914). **D** State 4-remains of loose setae are attached to minute segments of cuticle and jaw elements only are recovered (ROM-64915).

the product of dilute turbidity currents¹⁹ and thus the organisms were transported and experienced rapid burial^{14,19}. Following this, taphonomic studies used the high level of articulation of some fossil groups to suggest that minimal or no transport of the organisms took place²¹. However, more recently, the deposits were re-interpreted to be mud-rich slurry flows²⁰. There are potentially profound implications of such a slurry-type flow regime on the durability of soft-bodied organisms. We investigated this by integrating the study of Burgess Shale deposits with analog sedimentary process and taphonomic decay experiments to test the hypotheses that (i) the degradation of *Alitta virens* would increase with increasing flow duration and (ii) increasing the duration of pre-transport decay would also increase degradation. This is the first study that uses flume experiments calibrated with outcrop data to expand our understanding of the role of transport in the preservation of Burgess Shale organisms.

Results

Flow characteristics of the Burgess Shale Deposits at the Walcott Quarry. Our field observations indicate that individual beds typically comprise silt and clay with ‘floating’ quartz grains in places (100–500 µm but could reach up to 1000 µm). Deposits locally have erosive, scoured bases and contain sedimentary structures, such as parallel lamination, that are indicative of tractional sediment transport (Supplementary Figs. 2–5). The above sedimentary features indicate transitional cohesive flows; specifically, quasi-laminar to upper transitional plug flows²² that exhibit both turbulent and laminar characteristics and are capable of producing all of the features observed in the Burgess Shale deposits at the Walcott Quarry.

Effects of decay and transport on states of degradation. To quantify the combined effects of both pre-transport decay and flow duration on the carcasses of *A. virens*, we derived an index of degradation for this taxon (Fig. 1). In the experiments, specimens were decayed for 0, 24, or 48 h and then subjected to quasi-laminar to upper-transitional plug flows within an annular flume tank of durations of 25, 225, or 900 min. Untransported controls involved individuals that underwent static decay for the same total duration of pre-transport decay and transport as the relevant experimental treatment combination. Specimens of *A. virens* that experienced decay prior to transport ranged between whole and shrivelled to an unsupported gut with fluid escape and a general flattening of the body²³. Decay damage tended to occur towards

the posterior and mid-section of the polychaete. After transport, individuals were observed with their whole bodies still intact or with damage towards their posterior (state 1 and 2, Fig. 1a–b). Pre-transport decay has a significant effect on the state of degradation (ordinal logistic regression, $p < 0.001$). However, transport duration within a quasi-laminar to upper-transitional plug flow regime did not affect overall degradation (ordinal logistic regression, $p = 0.065$). Post-hoc Kruskal Wallis tests show that, for each combination of transported/non-transported and duration, the amount of pre-transport decay has a significant effect on the final state of degradation (Fig. 2 and Supplementary Table 1). For each amount of pre-transport decay, Mann-Whitney comparisons between transported treatments and non-transported controls reveal no significant difference in degradation (Supplementary Table 1).

Comparison with Burgess Shale Polychaete fossils. Examination of *Burgessochaeta* ($n = 154$) and *Canadia* ($n = 43$) from the Walcott Quarry of the Burgess Shale reveals that they are preserved as mostly pristine and undamaged with an average state of degradation of state 1 (Fig. 1a, Supplementary Data 1, Supplementary Fig. 8), and only limited specimens showed states 2 (20% of *Burgessochaeta* and 7% of *Canadia*) or 3 (4% of *Burgessochaeta* and 5% for *Canadia*) (Fig. 1b, c).

Discussion

The implications of the sedimentological transport processes that led to the preservation of the Burgess Shale biota in the Greater Phyllopod Bed are here analyzed for the first time through the integration of detailed sedimentological field observations, specimen analysis, and taphonomic flume experiments. Our results demonstrate that polychaetes of the Burgess Shale biota could potentially have been transported over substantial distances of at least 20 km. We interpret that the individual beds of the Greater Phyllopod Bed at the Walcott Quarry were deposited from quasi-laminar to upper-transitional plug flows and our results show that increasing transport duration in such flows does not cause significantly more damage to carcasses of *A. virens* beyond that already caused by decay. This is in contrast to turbulent flows that cause increasing damage with increasing transport duration²⁴. Intuitively, longer exposure times to pre-transport decay significantly affect the overall state of degradation, and this is consistent with other decay studies^{8,10,23,25}.

Fig. 2 Box and whisker plots showing states of degradation in respect to flow duration. The green boxplots (left) are the non-transported group and blue (right) are the transported groups. **A** 0-h pre-transport decay; **B** 24-h pre-transport decay; and **C** 48-h pre-transport decay. Error bars represent the range.

Comparison of our experimental results with observations of the states of degradation of fossil polychaete specimens from the Burgess Shale indicates that they were unlikely to have experienced significant decay before entrainment and entombment of their carcasses by sediment-gravity flows. The polychaete fossils are typically found compressed at different heights and orientations within the beds^{19,26} rather than occurring towards the base or top. This suggests they were transported and buried within a flow rather than being just buried by one. Reconstruction of the palaeo-oxygenation state at the Walcott Quarry is complicated²⁰, with geochemical data suggesting an oxic-anoxic boundary may have existed at the sediment-water interface²⁷. However, the paucity of bioturbation, including surficial trails and trackways, suggests predominant anoxic conditions and further argues against this being the original habitat of the organisms. Once the flow has ceased in our experiments, the sediment-water mixture remains as a soupy suspension, and we have observed that living *A. virens* can survive and escape in a functional state from these mixtures. This indicates that other polychaetes could potentially have also survived and escaped flows and their suspensions and

therefore that similar organisms of the Burgess Shale were most likely dead at the time of burial and probably upon incorporation into a flow. Together, the experiments and fossil analysis support a model for the deposits of the Greater Phyllopod Bed interval of the Burgess Shale where recently deceased animals could have been picked up and carried tens of kilometers by flows before being deposited and entombed^{19,20,28} (Fig. 3).

Our interpretation of the deposits from the Walcott Quarry combined with the recreation of flow conditions and taphonomic experiments with analog organisms sheds new light on the nature of the Burgess Shale and has implications for similar fossil assemblages. Burgess Shale-type lagerstätten are traditionally viewed as ‘windows’ into the biology and ecology of past life and are used to reconstruct in-life communities. This is based on the assumption that they have greater fidelity to a community than the normal fossil record due to the preservation of soft-bodied organisms. Our results show that the traditional interpretation of the Greater Phyllopod Bed assemblages as in-life communities may not be a faithful depiction, and this has potential implications for many Burgess Shale-type lagerstätten worldwide. Such

Fig. 3 Schematic flow reconstruction for the Walcott Quarry in the Burgess Shale. **A** Schematic Representation in which the laminar plug extends towards the base of the flow and changes to a transitional plug regime. A turbulent cloud of sediment is suspended in the water column above the plug flow. The soft-bodied organisms (labeled 1, 2, and 3) have been picked up along the flow path, potentially kilometers apart from one another. **B** Bed A from the Greater Phyllopod Bed of the Walcott Quarry. **C** Graphic log showing Bed A; soft-bodied organisms (1, 2, and 3) from the flow type above (**A**) will become mixed in the deposit. **D** Thin-section scan from Bed A showing parallel laminae, erosive, scoured bases, and “floating” quartz grains (Q). White arrows indicate transitional cohesive flow deposits.

fossil assemblages have been used to decipher Cambrian marine ecology and, in particular, community structure^{4–6,29}. The Cambrian Chengjiang and Qingjiang biotas of China, and Upper Ordovician Beecher's Trilobite Bed of the USA are widely interpreted to be emplaced by flows^{18,30,31} and transport of some organisms in the Cretaceous Jehol biota has been reported³². The degree to which taxa are retained, modified, or lost to the fossil record is critical to the key issue of what exceptionally preserved fossil deposits actually reveal about the biodiversity and evolution of ancient life. Little is known about how transport has biased the records and fidelity with which they reflect in-life palaeo-communities. Many of these assemblages may potentially record a seemingly complex palimpsest of several communities if preserved within the deposits of sediment-laden flows.

Konservat Lagerstätten capture decay-prone organic tissues and completely soft-bodied organisms alongside more routine fossils that comprise mineralized hard parts of animals and provide us with the most complete depiction of past life. The preservation of soft-tissued organisms in Lagerstätten is important because such sites offer valuable information on the retention of morphology, phylogenetics, and evolution of animals that are rarely preserved. However, what may be less certain is the true nature and paleoecological information locked up in such fossil assemblages. Robust paleoecological interpretations of Lagerstätten are important because many have been used to provide evidence of nature and tempo for significant events in the history of life on Earth. In order to test whether a fossil assemblage within a flow deposit does indeed represent an in-life community, it will be necessary to assess the relative durabilities of different benthic and nekto-benthic taxa that are preserved together. By using such a multidisciplinary approach we can gain a more holistic understanding of the sedimentary environment and establish criteria for determining whether transport-induced compositional biases occur and to what extent. Our results offer new views into this 'window' into the past and impact our understanding of the environmental framework of Burgess Shale-type deposits and the paleoecology of these extraordinary biotas.

Methods

Fieldwork and rock sample analysis. The primary objective of our fieldwork was to collect sedimentological data that would allow us to interpret the processes responsible for the deposition of the beds of the Greater Phyllopod Bed. These parameters could then be incorporated into our experimental design and recreation of Burgess Shale-type flows. To understand the complex sedimentary deposits of the Burgess Shale Formation, we targeted individual beds (Fig. 3, Supplementary Figs. 2–5) that were logged at outcrop for informative mm-scale and cm-scale sedimentary structures. Grain size analysis was conducted in the field using a grain-size comparator and hand-lens and during petrographic analysis. The Greater Phyllopod Bed has been logged in considerable detail in the field^{20,33}, and so logs produced from our work can be used to compare to previous studies. Detailed descriptions of the intervals sampled included color, bounding surfaces, micro-sedimentary structures, grain size, and textures. Larger-scale field mapping and analysis of sedimentary architecture were not undertaken and so we were not attempting to answer questions on the relationship of the Cathedral Escarpment to the fossil-bearing deposits or the precise provenance of the organisms.

We collected whole-rock samples from the Greater Phyllopod Bed of the Walcott Quarry at stratigraphic heights of 111.6, 136, 149.95, 184.83, and 226.68 cm (labeled Bed A to E, respectively) above the top of the Wash Limestone Member. All sedimentological samples for this study were collected in situ from this location under the Parks Canada collection and research permit (YNP-2015-19297). The permit for our fieldwork allowed us to collect and sample sedimentological material exclusively. These were subsequently sampled for laboratory analysis and thin-section preparation.

Petrographic analysis was performed on all samples using a Leica DM750P microscope. Each thin section was scanned with an Epson scanner to observe details of the millimeter-scale structures and textures (Fig. 3, Supplementary Figs. 2–5). Plain and cross-polarized light micrographs were taken of areas of particular sedimentological interest from each thin section and documented along with the petrological analysis. These samples were processed for further geochemical and elemental analysis.

Sample analysis. X-Ray Diffraction (XRD) was used to characterize the mineralogical content of the matrix of Bed A (111.6 cm above the top of the Wash Limestone Member) from the Walcott Quarry. For whole-rock bulk powder analyses, the sample was ground into a powder, and XRD was conducted using a PANalytical X'Pert3 diffractometer. For clay analysis, we applied the fractions to orientated glass slides. Organics were removed from each sample by H₂O₂ treatment before disaggregating the material using ultrasonic vibration. The suspended material was decanted from the ultrasonic bath in centrifuge bottles, which were topped up with deionized water so that each bottle weighed within the same gram. The bottles were placed in the centrifuge for two treatments, first at 1000 rpm for 4 min, and then again at 4000 rpm for 20 min. After the first treatment, the supernatant was transferred to new centrifuge bottles. The three lightest bottles were topped up with deionized water in order to reach the weight of the heaviest. The resultant concentrated sample yield (<2 µm clay) was used to conduct the clay analysis. Each sample slide was analyzed on the XRD in three states: after air-drying, glycol solvation, and heating to 550 °C³⁴. The clay minerals were identified from their characteristic basal reflections (001) in each state shown on the combined X-ray clay fraction diagram (Supplementary Note 1, Supplementary Fig. 7).

Energy-dispersive X-Ray spectroscopy (EDS-elemental mapping) was used to conduct an elemental analysis with a scanning electron microscope (SEM). We randomly selected and determined the relative abundance and distribution of elements in the matrix of Bed A (111.6 cm above the top of the Wash Limestone Member) (Supplementary Fig. 6). The thin-section sample was carbon-coated using an AGAR auto carbon coater before being placed into the SEM. The data was processed using Aztec Energy software and X-Ray maps were produced for Bed A.

Collection and Euthanasia of animals. We used the polychaete *A. virens* for this study as it is readily available, decays rapidly, and has been used previously to measure how far decay proceeded in the Burgess Shale^{5,21,35,36} to gain insights into static decay and preservation. These studies allowed us to rank the level of static decay³⁵ the polychaete had experienced before entering the treatments in this study. Degradation features of *A. virens* like posterior damage, disassociated setae, and how intact the overall organic remains were, could also be compared to the extinct polychaetes *Burgessochaeta* and *Canadia* from the Walcott Quarry.

Specimens of *A. virens* were bought live from a local bait shop in Southampton which sources their bait along the south-east coast of the UK. All were euthanized by exposure to anoxia for 60 min. Anoxic conditions were created by dissolving a SERA CO₂ tablet in 200 ml of artificial seawater²⁴. Pre-transport decay proceeded under oxic conditions to replicate an organism that had died in situ before being transported. Organisms were placed on a polyester mesh to help facilitate extraction¹⁰ and put into polyester containers with 200 ml of fresh artificial seawater. Containers were partially sealed to allow for slow oxygen diffusion³⁵. The polychaetes were left to decay at room temperature (~20 °C) for 0, 24, and 48 h. We assessed the level of decay³⁵ before the polychaete entered the annular flume for transport.

Flow Generation. The flume channel (160 l) was filled with a mixture of 11% kaolinite clay (Imerys Polwhite-E china clay, density: 360 kg/m³) and artificial seawater (6.67 kg of salt mixture that is mixed with 160 l tap water, Seamax, Peacock Ltd)^{24,37,38}. Characteristics of the deposits from the Burgess Shale suggest clay-rich flows transitional between turbulent and laminar that are consistent with the Upper Transitional Plug Flow (UTPF) and Quasi Laminar Plug Flow (QLPF) regimes of Baas et al. (2009). The requisite concentration of kaolinite and velocity needed to reproduce these flows were calculated from Sumner et al. (2009). An ultrasonic doppler velocity profiler (UDVP) was used to obtain a time-averaged velocity depth profile (MetFlow software and Microsoft Excel) and confirm the flow velocity (0.4 ms⁻¹) for our experiments (Supplementary Fig. 1).

Experimental protocol. Our experiments were designed to test the hypotheses that increasing pre-transport decay and transport duration (continuous predictor variables) under this flow regime would affect the state of degradation (Fig. 1; ordinal response variable) of the polychaete *A. virens*. Three conditions of flow duration of 25, 225, and 900 min (continuous independent variable 1) were used to test the effect of transport on the states of degradation. At the extreme, our flow durations corresponded to transport distances of 21.6 km. We hypothesized that the degradation to *A. virens* would increase over greater flow durations. Three conditions of pre-transport decay, 0, 24, and 48 h (continuous independent variable 2) were used to test the effect of increasing levels of decay on the states of degradation. We hypothesized that the longer exposure times to decay would result in greater degradation of the polychaete. For each treatment combination of pre-transport decay and transport, a set of controls was devised in which another polychaete was decayed for the same time but then placed in a polystyrene container filled with 11% kaolinite mixed in artificial seawater to mimic the contents of the annular flume. The polychaete remained static in the container for the equivalent flow duration as in the experimental treatment. All experimental and control treatments were repeated five times.

In order to address the degradation of soft-bodied organisms from the combined effects of decay and transport, other integral factors were considered but could not be generated in the laboratory conditions used for this study. Primarily,

the water temperature was contemplated during the design phases of this research. The counter-rotating annular flume tank is specifically designed to observe sediment-laden flows continuously along with the production of deposit type. It was not built with the capabilities to control water temperature, and as such, experiments were conducted at room temperature. All experiments were conducted under the same conditions and so any error will be systematic.

States of degradation. To quantify damage to *A. virens* from pre-transport decay combined with transport, we established an index of states of degradation (Fig. 1). The index provides an ordinal dependent variable for measuring damage after the combined effects of pre-transport decay and transport.

State 1 is a complete polychaete in which the entire body segment is intact. State 2 is damage towards the mid-section and the posterior transforms into tangled remains caused by the combination of transport and decay. The body remains intact as one segment. State 3 is the remains of the trunk and setae. The body structure has deteriorated significantly. State 4 is the remains of loose setae are attached to minute segments of cuticle and jaw elements only are recovered

Statistical analysis. Ordinal logistic regression was performed to determine the effect of increasing pre-transport decay and flow duration on the states of degradation of *A. virens*. A post-hoc Kruskal-Wallis *H* test was conducted to determine if there were overall effects of the amount of pre-transport decay for each transported and non-transported (control) duration. Subsequently, post-hoc, Mann-Whitney *U* tests were run to determine if there were differences between the transported and non-transported control groups at the equivalent durations of pre-transport decay and flow duration.

Museum work and comparison of experimental and fossil degradation.

Comparative fossil material for this study was examined at the Royal Ontario Museum, Toronto. All specimens were collected from the Greater Phyllopod Bed of the Walcott Quarry Shale Member by the Royal Ontario Museum field expeditions between 1993 and 2000. Details on the fossiliferous beds and polychaete specimens used in this study can be seen in Supplementary Data 1.

A total of 204 slabs containing 197 polychaete fossils (*Canadia* *n* = 43, *Burgessochaeta* *n* = 154) from beds throughout the Greater Phyllopod Bed were systematically surveyed for their degree of preservation after Caron and Jackson (2006), index of degradation (from this study), specimen length and any other notable features (coiled, dissociated setae etc.). Almost all specimens had slab counterparts and were counted only once. All polychaete fossils were macro-imaged using a Nikon camera and specimens with particular notable bodily damage were examined using a Nikon SMZ1500 microscope with an HR Plan Apo 0.5X WD 136 Nikon lens.

We compared our observed states of degradation in *A. virens* to the preservation of the anatomically similar fossil polychaetes *Burgessochaeta* and *Canadia* from the Greater Phyllopod Bed of the Walcott Quarry Shale Member of the Burgess Shale (Fig. 1, Supplementary Data 1).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The datasets generated and analyzed during the study are available in the Dryad repository, [<https://doi.org/10.5061/dryad.wdbrv15k0>].

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Author contributions

O.G.B.E., N.J.M., E.J.S., M.G.M., and L.A.B. conducted the fieldwork. O.G.B.E., N.J.M., and E.J.S. designed the experiments. O.G.B.E. undertook XRD and SEM-EDS analyses and interpretation. O.G.B.E. and N.J.M. imaged fossil specimens. O.G.B.E. performed the experiments, analyzed the data, and drafted the manuscript. N.J.M. was involved with the analysis and revising and editing of the article. E.J.S., M.G.M., and L.A.B. assisted with the revising and editing of the article. All authors gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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