Survival on a soft seafloor: life strategies of brachiopods from the Cambrian Burgess Shale

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ABSTRACT

Understanding the structure of benthic communities in the Cambrian remains a major challenge. Direct evidence for species interrelationships is rare and therefore past ecological interactions typically cannot be reconstructed with great accuracy. Here we reveal the community patterns and modes of life of brachiopods - one of the most

important filter-feeding groups of Cambrian ecosystems - from the Cambrian Burgess Shale Lagerstätte. Burgess Shale brachiopods attached to a range of hard substrates, including skeletal debris, conspecific brachiopods and enigmatic tubes, with an overwhelming preference for attachment on the demosponge *Pirania muricata*. The dominance of *P. muricata* as a substrate choice - even in bedding assemblages where *P. muricata* individuals are rare - and similarities to the gregarious attachment strategies of extant brachiopod species suggests that brachiopod larvae in the Burgess Shale community selected their attachment substrates. The distribution of brachiopod taxa is also intricately linked with the presence of suitable hard substrates, with species declining in bedding assemblages where their preferred hard substrates are absent. In addition, brachiopods in the Burgess Shale community are predominantly low epifaunal tierers and do not exploit niches high in the water column, despite the presence of suitable attachment sites. Our analysis of tiering height versus host height indicates that there is no selection by brachiopod larvae in regards to the height of attachment and individuals attached at the first point of contact with the selected substrate. Through comparisons with the 'early' Cambrian Chengjiang Biota, we confirm that by the 'middle' Cambrian (Series 3, Stage 5) brachiopods had already developed a range of attachment strategies similar to some modern brachiopod populations. Our results provide significant insight into the ecological constraints and adaptability of brachiopods in the earliest animal communities of the Cambrian.

Keywords: Palaeoecology, tiering, Lagerstätte, benthic, filter feeders, Cambrian Explosion

1. Introduction

Amidst the great radiation of animal life during the Cambrian, brachiopods were one of the first animal phyla to emerge, establishing themselves as one of the most important filter-feeding groups in Cambrian ecosystems (Pelman, 1977; Holmer et al., 1996; Ushatinskaya, 2008; Topper et al., 2013a; Skovsted et al., 2015). These bivalved lophophorates rapidly diversified and dispersed to all major palaeocontinental blocks by the third stage (ca. 520 Ma) of the Cambrian (Holmer et al., 1996; Brock et al., 2000; Ushatinskaya, 2008). As a result of their biomineralized valves, brachiopods are endowed with one of the most extensive and complete fossil records of any animal phylum (Sepkoski, 1981; Behrensmeyer et al., 2005), however, the rarity of preserved soft-tissues has impeded synecological studies and hindered key discussions regarding their early evolution. Knowledge of the group is heavily skewed towards their taxonomy and systematic relationships, based mainly on biomineralized characters, and substantial gaps exist in our knowledge of their ecology and interactions with other organisms.

Our understanding of the evolution and ecology of animals during the crucial Cambrian interval is largely driven by the examination of exquisitely preserved, soft-bodied organisms from a number of Burgess Shale-type deposits. The ‘early’ Cambrian Chengjiang Lagerstätte has provided much of our knowledge regarding the early ecology and adaptive morphologies of the Brachiopoda (e.g., Zhang et al., 2003; 2004; 2005; 2007a, b, c; 2008; 2009; Zhang and Holmer, 2013). Brachiopods from the ‘middle’ Cambrian Burgess Shale Lagerstätte have received little attention, with some exceptions (Holmer and Caron, 2006; Pettersson Stolk et al., 2010), since the original descriptions in the early 20th century (Walcott, 1912; Walcott, 1924). The

exceptional preservation and minimal transportation of the Burgess Shale community (Caron and Jackson, 2006) provides a superb opportunity to investigate the ecological interactions between brachiopods and their chosen substrates. Reports of direct ecological interactions between brachiopods, sponges, and the stem-mollusc *Wiwaxia* were first noted nearly three decades ago (Whittington, 1985; Conway Morris, 1985; Rigby, 1986) and only recently have such associations been given detailed consideration (Topper et al., 2014; Topper et al., 2015).

A change of ecological strategies in Cambrian echinoderms (Dornbos 2006; Zamora and Smith, 2010) and grazing molluscs (Bottjer et al., 2000; Dornbos et al., 2005, Caron et al., 2006; Smith, 2012) has been linked to the modification of substrate during the Cambrian, as increased endobenthic activity mixed and churned the Cambrian seafloor (Droser and Bottjer, 1989; Seilacher and Plüger, 1994; Seilacher, 1999 Bottjer et al., 2000; Dornbos et al., 2005; Dornbos, 2006; Álvaro et al., 2013; Kloss et al., 2015). The ecological response of Cambrian brachiopods to this change in substrate remains inadequately documented. Brachiopods have also been considered to contribute little to tiering complexity during the Phanerozoic (Bottjer and Ausich, 1986). Specimens attached to biological substrates suggest that brachiopods exploited and developed more variable levels of tiering in benthic communities than previously thought. It remains unclear, however, if attachment to a particular biological substrate is random or selective. Specifically, do brachiopods selectively settle on particular taxa to use as substrates or on particular body parts of these taxa (e.g., extremities)?

Here we provide the first detailed palaeoecological study of a Cambrian Lagerstätte brachiopod assemblage. Our main goal is to analyse brachiopod community patterns and modes of life to increase our understanding of the structure

and ecology of the Cambrian benthos. We focus specifically on the intimate relationship shared between brachiopods and their chosen substrates, given the importance of substrate as primary control on species distribution (Taylor and Wilson, 2003; Solan et al., 2004; Bromley and Heinberg, 2006), and investigate a relatively unexplored area, the evolution of tiering in Cambrian brachiopod communities.

2. Material and methods

2.1 Material

This study is based on 1422 brachiopod individuals representing seven brachiopod species from the ‘middle’ Cambrian (Series 3, Stage 5) Burgess Shale in British Columbia, Canada (Figs 1-8). The studied material is housed at the Royal Ontario Museum (ROM), the National Museum of Natural History of the Smithsonian Institution (USNM), and a small selection (all from the Phyllopod Bed) at the Geological Survey of Canada in Ottawa (GSC). Specimens predominantly come from the “thick” and “thin” expressions of the Stephen Formation (for the latter see Caron and Jackson, 2008) that crop out on Fossil Ridge and Mount Stephen in Yoho National Park (Fletcher and Collins, 1998). We focus on specimens from two stratigraphic intervals of the “thick” Stephen Formation, the Walcott Quarry Shale Member (WQ and BW prefixes, BW referring to the distance below the base of the Phyllopod Bed) and the slightly younger Raymond Quarry (RQ sample prefix) Shale Member (Fletcher and Collins, 1998). The majority of specimens were collected *in situ* within particular bedding assemblages or narrow stratigraphic intervals representing different burial deposits, but a number of specimens were also collected

from talus picking above (RT) and below (WT) the Walcott Quarry. In addition to the previous material, which was collected by the Royal Ontario Museum (ROM), original specimens from the so-called ‘Phyllopod Bed’ (locality 35k) were also examined (see Whittington, 1971; Caron and Jackson, 2006, 2008) and are part of the Walcott collection at the Smithsonian Institution (SI). In contrast with the ROM collections, the SI specimens represent assemblages of unknown duration, as precise stratigraphic provenance is unknown (Caron and Jackson, 2006, 2008). Additional material collected by the ROM from the Mount Stephen Trilobite Beds (ST), Oday Mountain (O, ODE, OR, ORU), Stanley Glacier, the so-called Tulip Beds (S7), and also from the Emerald Lake Oncolite Member were also examined (see Rigby and Collins, 2004 and O’Brien and Caron, 2012 for details on localities).

2.2 Methods

To analyze the extent to which brachiopods contributed to the tiering complexity of the Burgess Shale community, measurements were obtained from 96 brachiopod individuals from throughout the “thick” Stephen Formation. Tiering height was determined by measuring the distance between the lowermost margin of the chosen substrate, either a primary tierer (e.g., sponge or cancelloriid) or isolated sclerite (e.g., trilobite carapace) to the centre of the hinge line of the brachiopod individual (Fig. 9). This region represents the approximate position from where the pedicle would emerge and would correspond to the site of larval settlement and attachment. It is possible that some sponges may have been buried somewhat in the sediment during life (Rigby, 1986; Botting 2004, 2007). This is, however, difficult to quantify and, given the uncertainties surrounding the attachment mechanisms of

Cambrian sponges, the authors have chosen the lowermost margin to represent the site of attachment. Correct orientation for primary tierers was attained from spicule direction (monaxial spicules extending apically in *Pirania muricata* Walcott, 1920), expansion in body width towards the apical end (*Chancelloria eros* Walcott, 1920), presence of apical tufts (*Allonnia tintinopsis* Bengtson and Collins, 2015), and attachments to skeletal debris (*A. tintinopsis* and *P. muricata*; Figs 2F, 3L) indicating their attachment at the sediment-water interface (Bengtson and Collins, 2015).

The enigmatic tubes, *Tubulella* sp. and *Sphenothallus* sp. are interpreted as projecting vertically into the water column with the tapered end of the tube in contact with the seafloor (see Van Iten et al., 2002; Stewart et al., 2015). For brachiopod individuals attached on conspecific shells, it is interpreted that the conspecific shell being utilized as a substrate was standing upright at the sediment-water interface with the anterior margin of the attached brachiopod projecting into the water column, as is frequently the case in extant taxa (Fig. 7). It is possible that the gregarious conspecific shell clusters were attached to another substrate during life that would mean that the tiering results obtained herein represent minimum values. However, with no evidence to suggest what the individuals were attached to (e.g., *P. muricata* spicule or tissue remains) the authors have measured the tiering heights from the posterior margin of the brachiopod being utilized as substrate. Tiering heights, in some cases may also represent conservative measurements. Specimens of *P. muricata* (Figs 2E, 4L) and *Vauxia gracilentia* Walcott, 1920 (Fig. 2L-M), for example, are imperfectly preserved with incomplete basal margins. Seven *M. burgessensis* individuals (e.g. Fig. 2C-D, H-I) attached to isolated *P. muricata* spicules have not been included in the tiering analysis as they were most likely detached from a higher tiering position, rather than attaching to isolated *P. muricata* spicules on the seafloor. The presence of body wall

remnants on the basal margin of the isolated *P. muricata* spicules (Fig. 2D) is suggestive that the spicules were detached from the sponge during the burial process. It is interpreted that the majority of preserved attached brachiopods attached whilst the substrate was alive. Specimens that have affected the growth of the substrate (e.g., *Tubulella* sp., Figs 2N, 7G) or are preserved on opposing sides of the substrate (e.g., *Tubulella* sp., Fig. 2O) provides some evidence for this. However, hyoliths (Fig. 7K) and trilobite carapaces (Figs 2M, 4G-H) most likely represented debris on the seafloor. It is also possible that primary tierers in the Burgess Shale community were oblique (e.g., *C. eros*, *Tubulella* sp. and *Sphenothallus* sp.) rather than vertical to the seafloor during life. If this is the case, the measured heights may not provide an absolute value for height above the seafloor are a measure that can be directly compared with other tiering studies where tiering height was measured from the maximum length of the fossil (Ausich, 1980; Bottjer and Ausich, 1986; Clapham and Narbonne, 2002).

Brachiopod specimens were photographed under normal and cross-polarized light and wet and dry conditions using a Canon EOS6D digital SLR camera. Photographed images of each specimen were used to measure tiering heights and specimen size. EDAX elemental mapping was undertaken using a Zeiss Supra 35 VP microscope. Elemental mapping analyses were performed at an operating voltage of 15 kV, except for the analysis of carbon which was performed at 3 kV.

2.3 Analysis

To test if brachiopod epibionts either targeted specific heights above the sediment-water interface or preferentially attached at a specific height on a host substrate, we first measured the height above the sediment surface for all attached

brachiopods and the host maximum height for all specimens with attached brachiopod epibionts. For a brachiopod specimen to be included in our analysis, both brachiopod height and host height needed to be clearly established for that specimen (79 specimens out of our total of 96 specimens). We did not include specimens where the host is partially obscured by matrix or is fragmentary. These data were then used to calculate a ratio of brachiopod height to host maximum height, with all values converted to a percentage for further analysis.

If brachiopod epibionts preferentially attached at specific heights on the host substrate, the distribution of values for the ratio of brachiopod height to host maximum height should be non-uniform, indicating that all ratio values are not equally likely. To identify the potential data distribution, we first plotted our ratio data as both a histogram and using kernel density estimation. Kernel density estimation was used in addition to a histogram as, unlike a histogram, it is unaffected by bin size (Parzen, 1962). The kernel density bandwidth was estimated using the Silverman method (Silverman, 1986). These plots suggest either a uniform or a normal distribution (Fig. 13A), leaving the question of preferential tiering height unresolved. We therefore also used values for skewness and kurtosis, as proposed by Cullen and Frey (1999), to better identify the probability distribution that best fits our data (Fig. 13B). Possible parametric distributions were then fitted to the data using maximum likelihood estimation, and goodness of fit for each distribution was evaluated using the Kolmogorov-Smirnov test.

To explore potential substrate selectivity, we used the probabilistic model developed by Veech (2013) to test for statistically significant patterns of co-occurrence between brachiopod species and potential host taxa. This method uses presence/absence data to determine the probability that two species co-occur at a

frequency greater than or less than the observed frequency of co-occurrence if the two species were distributed independently of one another amongst a set of sites. These relationships where the probability of co-occurrence is at a frequency greater than the observed frequency are defined as positive; where the probability of co-occurrence is at a frequency less than the observed frequency, the relationship is defined as negative. All other relationships are considered random. We applied this technique to an updated version of the multivariate dataset of Caron (2005), with additional specimens added based upon new observations of previously unstudied material in the ROM collections (Supplementary Data 1.1), and with a focus on *Micromitra burgessensis*. The remaining brachiopod species are omitted in the probabilistic model, due to taxonomic uncertainties at the time when the original Caron (2005) dataset was gathered. Following Veech's (2013) model and Caron and Jackson (2008), we interpret each Burgess Shale bedding assemblage as a separate sampling site representing a single ecological snapshot of the community. Rare taxa (those with cumulative relative abundance of <0.5%) were removed for this analysis. All analyses were carried out using R 3.1.1 (R Development Core Team, 2013).

3. Background

3.1 Brachiopods of the "thick" Stephen Formation

The Burgess Shale brachiopod community has not been comprehensively investigated since the original taxonomic works of Walcott (1912, 1924) and the nomenclatural reevaluations of Resser (1938). Walcott (1924) initially described and illustrated six brachiopod species predominantly from the phyllopod bed on Fossil

Ridge; *Acrothyra gregaria* Walcott, 1924, *Micromitra zenobia* Walcott, 1924, *Micromitra (Iphidella) pannula* (White), *Lingulella waptaensis* Walcott, 1924, *Nisusia burgessensis* Walcott, 1924, and *Eoorthis bellicostata* Walcott, 1924. Walcott (1924) commented that brachiopods were rare in the British Columbian formations and the majority of species were described based on only a handful of specimens. In his series of contributions dealing with nomenclatural changes for Cambrian species, Resser (1938) reevaluated a selection of the Burgess Shale brachiopods, however, he possessed only limited material and no illustrations were provided. Only sporadic reports were published in the ensuing 60 years, until recently when the brachiopods of the “thick” Stephen Formation have gained renewed interest (Holmer and Caron, 2006; Pettersson Stolk et al., 2010; Topper et al., 2014, 2015).

Micromitra burgessensis is perhaps the most distinctive brachiopod taxon in the Burgess Shale, although it was originally described as *Micromitra (Iphidella) pannula* (White) by Walcott (1908, 1912) from the Trilobite Beds on Mount Stephen. The genus, *Micromitra* Meek, 1873, at the time was taxonomically problematic, consisting of three subgenera and twenty-six species, four of which had a number of subspecies with an additional single undetermined variant of a subspecies (Walcott, 1912, p. 336). These divisions were based nearly entirely on the character of the external ornament (Walcott, 1912, p. 336). The taxonomic division of the genus into subgenera and subspecies has for the large part been abandoned, and *M. (Iphidella) pannula* was redescribed by Resser (1938) who considered that only vague similarities existed with *Iphidella* Walcott, 1905, and erected a new species, *M. burgessensis*.

The combination of a diagnostic diamond-shaped ornament and exceptionally preserved, elongate chaetae that extend far beyond the mineralized shell make the

species instantly recognizable in the “thick” Stephen Formation. The possession of this remarkable chaetae and reports of the species attaching to *Pirania muricata* Walcott, 1920, have ensured that *M. burgessensis* has been frequently noted, albeit briefly, in many publications (Whittington, 1985; Conway Morris, 1986; Briggs et al., 1994; Rigby and Collins, 2004; Dornbos et al., 2005; Caron and Jackson 2006, 2008). However, a detailed examination of the species has only been undertaken recently (Topper et al., 2015).

Paterina zenobia was also originally assigned to *Micromitra* by Walcott (1912), based on specimens collected from the phyllopod bed and the eastern flank of Mount Stephen. Resser (1938) without explanation transferred the species to the genus *Paterina* Beecher, 1891. The generic transfer has been generally accepted (Caron and Jackson, 2008; Johnson et al., 2009; Topper et al., 2015) and was presumably based on the contrasting external ornament (prominent growth lines versus diamond shaped ornament), prominent growth lines being a characteristic feature more frequently observed in *Paterina* species compared with *Micromitra* species (Laurie, 2000). Both species are representatives of the Paterinata, a relatively small brachiopod lineage (14 genera in two families), that were the first brachiopods to emerge from the Cambrian Explosion and range through to the late Ordovician (Williams et al., 1998; Laurie, 2000).

Organophosphatic linguloid brachiopods are common constituents of Cambrian brachiopod assemblages, and *Lingulella waptaensis* Walcott, 1924, represents the most abundant brachiopod species in the Walcott Quarry Shale Member. Published records of *L. waptaensis* have been rare since the original description. Recently, the taxon has been revised in detail by Pettersson Stolk et al. (2010). Shell structure analysis confirmed earlier investigations (Conway Morris,

1990; Briggs et al., 1994) that *L. waptaensis* retained its phosphatic composition and for the first time, pedicle-bearing specimens were described and illustrated (Pettersson Stolk et al., 2010). Walcott (1919) and Pettersson Stolk et al. (2010) both suggested that *L. waptaensis* was suspended above the sediment-water interface during life with its pedicle embedded into the soft sediment or onto sediment covered by colonies of the cyanobacterium *Morania*.

Acrothyra gregaria was first described by Walcott (1924), however the description is cursory and Walcott (1924) did not even designate a holotype. The small size (< 2 mm in length and width, frequently < 1 mm) undoubtedly hindered Walcott's (1924) diagnosis, and key morphological characteristics were not observed. Walcott (1924) considered the species to be similar to several species of *Acrotreta* Kutorga, 1848. However, the compressed nature of the valves that has consequently obscured the pedicle foramen and the lack of internal information prohibit detailed comparison (Topper et al., 2013b). Acrotretids arose in Stage 3 of the Cambrian (Holmer and Popov, 2000; Ushatinskaya, 2010) and rapidly became not only one of the most generically diverse brachiopod orders in the late Cambrian but also one of the most abundant, occurring in huge numbers, particularly in carbonate settings (Ushatinskaya, 2010). *Acrothyra gregaria* also occurs in relatively high numbers in the Walcott Quarry Member and can be frequently observed canvassing large slabs of excavated rock. Consequently, *A. gregaria* has been previously interpreted as living in clusters on the Burgess Shale seafloor, partially buried in the seafloor with only the ventral valve exposed (Briggs et al., 1994).

The kutorginid *Nisusia* is a brachiopod genus that is a relatively common representative of early to middle Cambrian shelly faunal assemblages (Popov and Williams, 2000). Originally described as *Orthisina alberta* (Walcott, 1886), the taxon

was later renamed without explanation as *Nisusia alberta* (Walcott, 1905). Specimens of this species identified from the Walcott Quarry Member by Walcott (1912) were later redescribed as *N. burgessensis* (Walcott, 1924). *Nisusia burgessensis*, like *M. burgessensis*, has been documented attached to the spicules of *P. muricata* (Whittington, 1985; Briggs et al., 1994) but also to the scleritome of the stem-mollusc *Wiwaxia* (Conway Morris, 1985; Topper et al., 2014). A single specimen of *N. burgessensis* illustrated by Walcott (1924, plate 110:1) and reproduced here (Fig. 3E) exhibits 10 long, marginal structures that have been previously interpreted as chaetae (Walcott, 1924; Briggs et al., 1994). The structures do resemble in length and shape to *M. burgessensis* chaetae, however their incomplete and irregular nature suggests some level of decay and disassociation, and therefore they are unlikely to be related to *N. burgessensis* (Holmer and Caron, 2006; Topper et al., 2014). Consequently, soft-part preservation remains to be observed in this species.

The genus *Diraphora* was erected by Bell (1941) to include a number of Cambrian North American species formerly referred by Walcott (1905, 1924) to the genera *Billingsella*, *Eoorthis*, *Wimanella*, and *Protorthis*. The species *Eoorthis bellicostata* Walcott from the “thick” Stephen Formation and the Meagher Formation of Montana was selected as type species of *Diraphora*. *Diraphora bellicostata* represents the only rhynchonelliform brachiopod in the “thick” Stephen Formation, but is particularly difficult to accurately identify, as the defining morphological features, such as the teeth and musculature, have been eliminated by the flattened, carbonaceous nature of the preserved specimens. Consequently, the valves strongly resemble those of *N. burgessensis*. This task is not made any easier because both species exhibit a similar ornament. In the absence of distinguishing morphological features, the diagnostic subquadrate outline of *D. bellicostata* differentiates the genus

from the rectangular or semiovoid outline characteristic of *N. burgessensis* (compare Popov and Williams, 2000, fig. 130.1 with Williams and Harper, 2000, fig. 528.1).

Acanthotretella spinosa Holmer and Caron, 2006, was described recently based on 42 specimens predominantly recovered from the Great Phyllopod Bed (Holmer and Caron, 2006). Contrasting with the other brachiopods known from the “thick” Stephen Formation, the valves of *A. spinosa* are frequently deformed, prompting Holmer and Caron (2006) to suggest that the valves were entirely organic or potentially had a minor mineral component. A single specimen of the pedunculate brachiopod was first illustrated by Jin et al. (1993, fig. 3:6) as *Lingulella* sp., however, the presence of long, slender spines that cover and penetrate the shell easily distinguish *A. spinosa* from *Lingulella*. Holmer and Caron (2006) described *A. spinosa* as a stem group brachiopod, but Hu et al. (2010) tentatively assigned the genus to the Siphonotretoidea after describing a new species, *A. decaius* Hu, Holmer and Skovsted, 2010, from the early Cambrian Guanshan fauna of Yunnan, China.

3.2 Depositional environment

The “thick” Stephen Formation represents a relatively deep-water depositional setting situated at the base of the Cathedral Escarpment (Fritz, 1971). The presence of an endofauna (e.g., priapulids, polychaetes) and the prevalence of sessile organisms such as brachiopods, some sponges (e.g., Fig 2D), and cancelloriids (Bengtson and Collins, 2015) attached to hard substrates suggest that the original Burgess Shale seafloor was not a firmground substrate as in other contemporaneous Cambrian localities (Droser et al., 2002; Tarhan and Droser, 2014), although the presence of grazers suggests that some areas were dominated by microbial mats (Caron et al.

2006). Remains of organisms are considered to have been buried catastrophically, most likely as a result of high-density fluidized mud-flows (Allison and Brett, 1995; Gabbott et al., 2008; Gaines, 2014), rather than storm-generated back-currents (Aitken and McIlreath, 1990; Gostlin and Miall, 2005) or turbidites (Piper, 1972; Orr et al., 1998). The amount of transport and the conditions for preservation in the post-burial environment have been, and still are, a matter of debate. Many authors consider benthic anoxic conditions a prerequisite to the exceptional preservation seen in Burgess Shale-type deposits and, consequently, fossil assemblages have been interpreted to be transported into an anoxic setting before preservation (Conway Morris, 1986; Allison, 1988; Butterfield, 1995, 2003; Gaines et al., 2005, 2012; Gaines and Droser, 2010; Gaines, 2014). Other authors consider the presence of burrows, *in situ* molts, and census assemblages preserved together with time-averaged assemblages together, to be indicative of no or limited transport of the community along the basinal edge of the Cathedral Escarpment (Caron and Jackson, 2006; Haug et al., 2013; but also see Gaines, 2014) and possible deposition under a fluctuating oxycline with intermittent oxygenated bottom water conditions (Powell et al., 2003; Forchielli et al., 2014).

The presence of chaetae-bearing brachiopod specimens preserved attached to a variety of substrates, including sponges (Figs 2-4, 8), indicates that if the assemblage was transported, transportation was minimal. We therefore consider brachiopod specimens preserved with chaetae and attached to substrates to represent individuals buried alive and having undergone limited or no transportation (see also Caron and Jackson, 2006).

4. Results

4.1 Preservation, taphonomy and community composition

Brachiopod specimens in the “thick” Stephen Formation exhibit a variety of preservational types. Calcitic or weakly biomineralized brachiopod species such as *Nisusia burgessensis* Walcott, 1924, (Fig. 5B) and *Diraphora bellicostata* (Walcott, 1924) are preserved as flattened, carbonaceous films with some specimens showing weak topographical relief. *Acanthotretella spinosa* exhibits evidence of soft-deformation and was most likely weakly mineralized (Holmer and Caron, 2006). Original calcium phosphatic brachiopod species, such as the paterinids, *Micromitra burgessensis* Resser, 1938, and *Paterina zenobia* (Walcott, 1912) and the lingulid, *Lingulella waptaensis* Walcott, 1924, (see Pettersson Stolk et al., 2010) display topographical relief and have retained their calcium phosphate shells (Fig. 5A, C-D). Chaetae were originally preserved in carbon (Fig. 5C, D) and have been replicated by a variety of elements, including iron (Fig. 5A, C-D) and calcium (Fig. 5D), probably during late diagenesis (Butterfield et al., 2007). The lack of sulfur in the samples indicates that the iron is more likely present as iron oxide rather than pyrite. Because the specimens that have been examined in this study and in previous studies come from a variety of horizons within the “thick” Stephen Formation, variations in elemental composition between specimens are attributed to variations in preservational microenvironments and possibly to various degree of weathering, especially for material collected on talus slopes.

The Burgess Shale fauna exhibits a high degree of brachiopod disparity, with seven species from six different orders (Walcott, 1924; Resser, 1938; Holmer and Caron, 2006; Hu et al., 2010; Pettersson Stolk et al., 2010). Soft-part preservation is

only observed in four species. Two species are preserved with the pedicle intact, *A. spinosa* and *L. waptaensis*, and only two species can be confidently recognized as possessing chaetae: the paterinate brachiopods *M. burgessensis* (Fig. 2) and *P. zenobia* (Fig. 4E-J). The brittle spines that cover the shell of *A. spinosa* are not considered to be homologous to chaetae (Holmer and Caron, 2006). The faint outline of a visceral cavity and umbonal muscle in a few specimens of *A. spinosa* and *L. waptaensis* has been noted by Holmer and Caron (2006) and Pettersson Stolk et al. (2010). The remaining three species, *N. burgessensis*, *D. bellicostata* and *Acrothyra gregaria*, do not show any discernable soft-tissue details.

The brachiopod communities from the Walcott Quarry Shale Member and the overlying Raymond Quarry Shale Member, despite their close stratigraphic and geographic proximity, display a high degree of discrepancy (Fig. 1A). *Micromitra burgessensis*, readily identifiable from its distinctive diamond-shape ornament (Fig. 2), and the kutorginid *N. burgessensis* (Fig. 3) are the only species present in both localities (Fig. 1). *Micromitra burgessensis* is abundant in the Walcott Quarry Shale Member (Fig. 1B) and dominates the Raymond Quarry Shale Member, where the species constitutes 99% of the brachiopod community. *Nisusia burgessensis* is common in the Walcott Quarry Shale Member (Fig. 1A) but is only a minor component in the Raymond Quarry Shale Member fauna. Only two specimens of *N. burgessensis* are documented in the ROM collections of the Raymond Quarry (Fig. 3L-M), although this may be because brachiopods were rarely collected (Devereux, 2001) and a detailed inventory of the fauna is still lacking. *Paterina zenobia* has been recovered from talus material above the Walcott Quarry Shale Member, suggesting provenance from the overlying Raymond Quarry Shale Member (e.g., Fig. 4G-H) or from shale members above it, but there is no known record of *in situ* material in the

ROM Raymond Quarry collection. *Lingulella waptaensis* is the most abundant brachiopod species in the Walcott Quarry Shale Member, followed by *A. gregaria*, *N. burgessensis*, and *M. burgessensis* (Fig. 1B). These four species are recurrent across a large number of bedding assemblages throughout the Walcott Quarry Shale Member (Caron, 2005), suggesting that they could adapt to a wider variation of abiotic and/or biotic conditions compared to the rarer and relatively restricted species, *D. bellicostata* (occurring in at least three bedding assemblages) and *A. spinosa* (occurring in five bedding assemblages; Holmer and Caron, 2006).

4.2 Brachiopod attachment strategies

4.2.1 *Micromitra burgessensis*

Micromitra burgessensis is also the most commonly preserved brachiopod taxon attached to hard substrates (Figs 2, 6). Disregarding the two small slabs from the Raymond Quarry Shale Member that yield 164 dissociated, isolated, fragmentary valves, 30% of all *M. burgessensis* individuals (64 out of 215 individuals) are preserved attached to a range of biogenic substrates (Fig. 2). Approximately 50% of specimens (103 individuals) are preserved with chaetae and it is possible that the remaining specimens that do not exhibit chaetae were buried after the individual had died. Unlike *A. spinosa* and *L. waptaensis*, *M. burgessensis* does not possess a long pedicle (relative to shell length). Instead, individuals attach via a short, pad-like pedicle, their hinge frequently juxtaposed parallel to the substrate (Fig. 2L-O) and their pedicle obscured by their homeodeltidium (Fig. 2P). The high abundance of *M. burgessensis* specimens still attached to their respective substrates suggests the

species' pedicular attachment was relatively solid in comparison to the other brachiopod species present in the community.

The spicules of *Pirania muricata* are the preferred substrate overall, with over half the attached *M. burgessensis* specimens (52%) associated with this sponge, followed by attachments to conspecific brachiopod valves (14%), the enigmatic tube *Tubulella* sp. (11%), *Allonia tintinopsis* Bengtson and Collins, 2015 (10%), and a range of other sponge and skeletal elements (Fig. 6). Attached *M. burgessensis* specimens are primarily preserved with chaetae (76% of attached individuals), providing robust evidence for burial whilst the individuals were alive. The absence of chaetae in the remaining attached specimens may be potentially due to concealment by adjacent faunal specimens or angled in such a manner that they remain hidden in the matrix. *Micromitra burgessensis* individuals in the Walcott Quarry communities are predominantly preserved attached to *P. muricata* (86%), with only a small number attached to hyolith and trilobite skeletal debris (Fig. 6A).

In the older Walcott Quarry Shale Member community, specimens of *M. burgessensis* are preserved attached to conspecific shells (33%), *Tubulella* (29%), *Allonia tintinopsis* (29%), and the sponge *Vauxia gracilenta* (9%). The large majority (89%) of attached specimens of *M. burgessensis* display a solitary lifestyle (as the only organism attached to that particular substrate; Figs 2A-M, 7) or as conspecific clusters of individuals (Figs 2N-P, 7). Only 7 individuals (11%) are preserved attached on a substrate together with other brachiopod species (Fig. 8).

4.2.2 *Nisusia burgessensis*

Nisusia is exclusively known from its shell morphology, despite reported occurrences in deposits of exceptional preservation, such as the Kaili Biota (Huang et

al., 1993; Zhao et al., 2005; Mao et al. 2014), the Balang Formation (Peng et al., 2005; Liu and Lei, 2013), and the Burgess Shale (Walcott, 1924; Briggs et al., 1994; Topper et al., 2014). Only 25 specimens (10% of the total individuals) of *N. burgessensis* are preserved attached to hard biological substrates, suggesting that the pedicle may have been relatively tenuous, with specimens detaching during the burial process or the pedicle decaying rapidly upon burial. Attachment to the spicules of the sponge *Pirania muricata* is most common (16 specimens - 64%). Three specimens (12%) are attached to *Wiwaxia corrugata* sclerites (Topper et al., 2014) and three specimens (12%) to a single specimen of the enigmatic *Sphenothallus* sp. (Van Iten et al., 2002; fig.1.3-1.4). The remaining three specimens (one specimen on each substrate type) are attached to *Hazelia* sp. (Fig. 8J-K), *A. tintinopsis* (Fig. 3L-M), and a tube belonging to *Selkirkia columbia* Conway Morris, 1977 (Fig. 3I). *Nisusia burgessensis* does not display the same consistent conspecific clustering that is prevalent in *M. burgessensis*, with one *P. muricata* specimen found in the Walcott Quarry Shale Member hosting three *N. burgessensis* individuals (Fig. 8A-E) and three *N. burgessensis* individuals collected from the Mount Stephen Trilobite Beds attached to a single representative of *Sphenothallus* (Van Iten et al., 2002; fig.1.3-1.4). There are no examples of *N. burgessensis* attached to other *N. burgessensis* specimens. Individuals of *N. burgessensis* do co-occur on *P. muricata* with *M. burgessensis* and *A. gregaria* (Fig. 8), although more than half of the overall attached individuals (60%) exhibit a solitary lifestyle. Only two specimens of *N. burgessensis* have been documented from the Raymond Quarry Shale Member and only one of them is preserved attached to a substrate, in this case *A. tintinopsis* (Fig. 3L-M).

4.2.3 *Acrothyra gregaria*

Acrothyra gregaria is the second most abundant brachiopod species in the Walcott Quarry Shale Member (behind *L. waptaensis*); however, only 13 specimens (5% of total individuals) are preserved attached to a substrate (Figs 4A-D, 6).

Acrothyra gregaria displays a fairly limited array of attachment strategies, only preserved attached to *P. muricata* (10 specimens) and *Chancelloria eros* Walcott, 1920 (4 specimens; see Bengtson and Collins, 2015, fig. 9). Acrotretids are most commonly isolated by acid maceration from carbonate deposits (e.g. Bell, 1948; Holmer, 1989; Popov and Holmer, 1994) and, consequently, their palaeoecology and life habits have remained speculative. *Acrothyra gregaria*, as the name suggests, has been interpreted as living in clusters on the Burgess Shale seafloor, a perception seemingly based entirely on samples yielding large numbers of *A. gregaria* valves in close association (Walcott, 1924), presumably transported and buried after death.

The acrotretid pedicle is known from only a single species, *Kuangshanotreta malungensis* Wang, Zhang, Holmer, Hu, Wang and Li, 2012, documented from the Cambrian Chengjiang Lagerstätte (Wang et al., 2012). *Kuangshanotreta malungensis* possesses a thin (approximately 100 µm in width), thread-like pedicle that protrudes from a small posteriorly located foramen (Wang et al., 2012). The size of the pedicle foramen (and presumably the pedicle) does vary between acrotretid genera (ranging from approximately 30 – 120 µm in width; see Bell, 1948; Holmer, 1989; Popov and Holmer, 1994; Streng, 1999; Holmer and Popov, 2000; Streng and Holmer, 2006; Topper et al., 2013b, c) and, although the pedicle foramen of *A. gregaria* cannot be distinguished, the similarities in shell length and width with *K. malungensis* supports the presence of a similar-sized pedicle foramen in *A. gregaria* (compare Wang et al. 2012 and Figs 4A-D, 8E-L). The close juxtaposition of *A. gregaria* specimens to their substrate (Figs 4A-D, 8E-L) demonstrates that their pedicle was relatively short.

Given their diminutive size and short pedicular attachment it is extremely doubtful that *A. gregaria* attached directly to the fine-grained Burgess Shale substrate. Attachment directly at the sediment-water interface would leave them susceptible to the movements of larger epibenthic grazers and even the slightest disturbance would have effectively covered the individual with sediment, limiting food intake and respiration and ultimately leading to the death of the organism. The combination of small body size and an attachment via a thin pedicle suggests that *A. gregaria* individuals could have been easily dislodged from their respective perches, explaining the low numbers of recorded specimens preserved attached to hard substrates. *Acrothyra gregaria*, *K. malungensis*, and possibly *Ottenbyella ibexiana* Holmer, Popov, Streng and Miller, 2005, are the only acrotretid brachiopods documented in life position, and interpretations of acrotretid brachiopods anchored directly to the substrate are purely conjectural (e.g., Henderson and Dann, 2010). It is therefore reasonable to assume that, despite of the low percentage of *A. gregaria* individuals preserved attached to substrates in the Burgess Shale, *A. gregaria* individuals required attachment to hard substrates for survival and the relatively low numbers are largely due to taphonomic bias.

4.2.4 *Diraphora bellicostata* and *Paterina zenobia*

Both *D. bellicostata* and *P. zenobia* represent relatively rare species in the “thick” Stephen Formation. Only 9 specimens of *D. bellicostata* have been documented from the this formation and only 6 from the Walcott Quarry Shale Member. Two individuals are attached to a spicule from a fragmentary specimen of *P. muricata* (Fig. 4K-L), and both specimens are from talus material.

Paterina zenobia broadly resembles *Micromitra burgessensis*, not just in general shell morphology and the possession of elongate chaetae (see Topper et al., 2015; fig. 4), but also mode of attachment (a short, pad-like pedicle). *Paterina zenobia* is only known from talus material, predominantly from the Mount Stephen Trilobite Beds (ST), Odaray Mountain (O, ODE, OR, ORU), Stanley Glacier, the so-called Tulip Beds (S7), and, talus immediately overlying the Walcott Quarry (most likely derived from the Raymond Quarry Shale Member). There are a total of 74 specimens of *P. zenobia* in the “thick” Stephen Formation. Twenty (27% of total individuals) have been preserved with identifiable chaetae and only 8 (11% of total individuals) have been preserved attached to some form of hard substrate (Fig. 4E-J). The majority of specimens appears to have been severely weathered (found in talus, so probably a result of transport and exposure, Fig. 4E-F) and are fragmentary (especially the Mount Stephen talus material). It is likely that morphological and ecological information has been lost as a result. From the available material, *P. zenobia* appears to show gregarious behaviour analogous to *M. burgessensis*, with the large majority (75% of attached specimens) sharing a hard substrate with another *P. zenobia* individual (Fig. 4E-I). Not all substrates could be accurately identified (Fig. 4I-J), with conspecific shells and trilobite skeletal debris hosting two individuals each (Fig. 4E-H) and one small specimen attached to a spicule of a fragmentary *P. muricata*. *Paterina zenobia* does appear to show a similar attachment strategy to *M. burgessensis*, however, the lack of faunal association due to talus-based material prohibits a more detailed analysis.

4.2.5 *Acanthotretella spinosa* and *Lingulella waptaensis*

The attachment strategy of the pedunculate brachiopods *A. spinosa* and *L. waptaensis* is unclear. Both taxa possess long and slender pedicles, ranging from a maximum of twice the valve length in *L. waptaensis* (Pettersson Stolk et al., 2010) to four times the valve length in *A. spinosa* (Holmer and Caron, 2006). Despite the abundance of *L. waptaensis* in the Walcott Quarry Shale Member (396 specimens) only 3 individuals have been preserved with pedicles (maximum length of 16.48 mm and width of 0.3 mm) and none are found attached to a substrate (Pettersson Stolk et al., 2010). The pedicle of *A. spinosa* is much more frequently preserved and is present in most specimens (90% of total individuals), reaching a maximum length of 25 mm and width of 0.4 mm (Holmer and Caron, 2006). One specimen of *A. spinosa* is preserved with its pedicle looping under an antenna of a *Sidneyia* carcass (Holmer and Caron, 2006; fig. 12C-D). The terminal end of the pedicle is concealed by sediment and the specimen could represent a fortuitous superposition between the two organisms (as discussed by Holmer and Caron, 2006). A cluster of six specimens with pedicle preserved overlying an unidentified organic structure prompted Holmer and Caron (2006; fig. 12A-B) to suggest that *A. spinosa* anchored itself preferentially to a seafloor that was covered by sheet-like colonies of the cyanobacterium *Morania*. A similar strategy was suggested for *L. waptaensis* based on the frequent co-occurrence of the species with *Morania* in the Walcott Quarry Shale Member (Walcott, 1919; Pettersson Stolk et al., 2010). A second species of *Acanthotretella*, *A. decaius* Hu, Zhang, Holmer and Skovsted, 2010, documented from the Guanshan Fauna of China, failed to shed any light on the attachment strategy of this brachiopod genus. No direct evidence has been found herein to further elucidate the attachment strategy of either *A. spinosa* or *L. waptaensis*.

4.3 Tiering of the Burgess brachiopod communities

Bottjer and Ausich (1986) divided epifaunal tierers into two major groups, primary and secondary tierers. Primary tierers represent organisms whose bodies are in direct contact with the sediment-water interface, and secondary tierers are organisms that maintain positions above or below the sediment-water interface by attaching to primary epifaunal tierers or living in the burrows of primary tierers (Bottjer and Ausich, 1986; Ausich and Bottjer, 2001). Primary and secondary tierers in Proterozoic assemblages can then be classified into three epifaunal tiering subdivisions: low (0 to +50 mm), medium (+50 to 200 mm) and high (+200 to 750 mm) (Bottjer and Ausich, 1986; Ausich and Bottjer, 2001). The large majority of the brachiopod individuals in the “thick” Stephen Formation can be classified as low epifaunal tierers, confined to within 50 mm above the sediment-water interface (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986; Ausich and Bottjer, 2001). The only exceptions are two *A. gregaria* specimens that would be technically classified as medium level secondary tiers, perched 50.7 mm and 52.2 mm above the sediment-water interface. This outcome is in agreement with earlier studies that emphasize that brachiopods contribute little to tiering complexity in the Palaeozoic (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986). This, however, is a rather rudimentary classification, a paradigm that only equates maximum height above the sediment-water interface with tiering complexity. This inference was based predominantly on the development of primary tierers with only minimal information available on secondary tierers (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986). As tiering is the vertical distribution of organisms, attention should be given to the distribution and interaction between tiered organisms in the community, not exclusively maximum height above and/or below the seafloor. The brachiopods in the Burgess Shale

community do not display a high concentration of individuals at a single tiering level, instead exhibiting a noticeably even distribution and partitioning of resources, despite the low tiering levels attained.

Micromitra burgessensis and *Nisusia burgessensis* individuals dominate the dataset for tiered brachiopods in the “thick” Stephen Formation, with the remaining three brachiopod species (*A. gregaria*, *D. bellicostata*, *P. zenobia*) examined constituting less than 20% of the total tiered specimens. The large majority of brachiopods (84%) in the “thick” Stephen Formation occupy a tiering interval of 0-16 mm above the sediment-water interface (Fig. 10). Within this 16 mm interval, total tiering heights are relatively evenly distributed (Fig. 10) and all five brachiopod species are represented (Fig. 10). *Micromitra burgessensis* is commonly attached within the 10 mm interval above the sediment-water interface (32 specimens in total), with a general decrease in numbers above this tiering height. Individuals of *N. burgessensis* are absent from the lowest tiering levels (0-2 mm) and are best represented in the 10-12 mm tiering bracket, where six individuals are recorded. The three remaining brachiopod genera, *A. gregaria*, *P. zenobia* and *D. bellicostata*, are represented by few individuals (21 between the three species) and frequently occur in the lower tiered levels (Fig. 10). *Acrothyra gregaria* displays a wide range of tiering heights, from individuals recorded immediately above the sediment-water interface to individuals attached to the apical part of a *C. eros* individual at 52.2 mm above the seafloor (Bengtson and Collins, 2015; their fig. 9). There is a dramatic decrease in individuals occupying tiering levels higher than 16 mm (16 individuals in total), with the aforementioned *A. gregaria* specimen reaching the maximum height above the sediment-water interface at 52.2 mm. The maximum tiering height occupied by *N. burgessensis* and *M. burgessensis* individuals is 27.5 mm (Fig. 10).

With the exception of the dramatic decrease of brachiopods in tiering heights over 16 mm above the seafloor, tiering boundaries appear relatively consistent. For example, individuals of *N. burgessensis* are absent immediately above the benthic boundary layer (tiering interval 0-2 mm), however, this is the preferred tiering interval of *A. gregaria* (Figs 4A-D, 10). The tiering heights of *M. burgessensis* and *N. burgessensis* also appear to complement each other, (Fig. 10). Peak tiering heights of the two genera are slightly offset, and at intervals where the number of *M. burgessensis* individuals is fewer, specimens of *N. burgessensis* increase in prominence (Fig. 10). Tiering strategies are perhaps best illustrated on substrates that host more than a single brachiopod individual (Fig. 8). On these substrates, brachiopod specimens are attached at a variety of heights on different locations of the chosen substrate (Fig. 8).

Individual brachiopod taxa in the “thick” Stephen Formation also exhibit a considerable degree of tiering flexibility. Species can occur at a variety of tiering heights in different bedding assemblages or in multiple tiers in a single bedding assemblage. For example, twelve individuals of *Nisusia burgessensis* occur in one bedding assemblage (BW-150), all attached to *Pirania muricata*. These individuals exhibit tiering heights ranging from 2.2 mm to 15.2 mm. *Micromitra burgessensis* also doesn’t exhibit any distinct tiering preferences, with individuals recorded at a range of heights across the “thick” Stephen Formation and lacking any sign of tiering specialization. The acrotretid brachiopod, *A. gregaria*, although not confined to the lowest tiering interval (0-2 mm), does appear to exhibit a preference for relatively low tiering levels (Fig. 10), yet can also attach to *C. eros* and achieve relatively high tiering levels (Bengtson and Collins, 2015, fig. 9). Both *P. zenobia* and *D. bellicostata*

also seemingly attach at the lower tiering intervals, but the rarity of preserved specimens shrouds their exact tiering preferences.

Both the histogram and kernel density estimation for the ratio of brachiopod height to host substrate maximum height show a concentration of values at 50% of host maximum height (Fig. 13A). Whilst this is a possible indication that the distribution is normal, the spread of the remaining values could equally represent a uniform distribution. Values for skewness (0.137) and kurtosis (2.145) suggest a uniform, normal, or beta distribution (Fig. 13B). Testing goodness of fit for all three distributions, the distribution of the height ratio data is significantly different from both a normal and a beta distribution (Kolmogorov-Smirnov $P < 0.05$) but cannot be distinguished from a uniform distribution (Kolmogorov-Smirnov $P > 0.05$). There is therefore no indication that brachiopod epibionts are concentrated at specific heights on the host substrate.

Our co-occurrence analysis indicates that many other potential attachment substrates co-occur with *M. burgessensis* at a frequency greater than would be expected, in the Walcott Quarry Shale Member (a positive result in our Veech analysis – Supplementary Data 1.1). This means that *M. burgessensis* had consistent access to a variety of potential attachment substrates, such as *Tubulella* sp., *Chancelloria* sp., and *Vauxia* spp. in the Walcott Quarry Shale Member. The prevalence of *M. burgessensis* specimens attached to *P. muricata* therefore suggests some degree of substrate selectivity.

5. Discussion

5.1 The search for stability

The primary focus of many living brachiopods is to attach to a hard substrate and retain the ability to feed efficiently (e.g., James et al., 1992). The soft, muddy Burgess Shale seafloor provided limited hard substrata, in conjunction, with the presence of destabilized and suspending sediment caused by weak bottom currents and the movement of benthic organisms (such as *Wiwaxia corrugata* and *Odontogriphus omalus*) would have made this focus a challenging prospect. The intimate relationship between attachment substrates and the distribution of brachiopods becomes apparent when comparing the Walcott Quarry brachiopod community to the Raymond Quarry brachiopod community (see reconstructions in Figs 14, 15). The most probable reason for the observed discrepancies in attachment strategies is the absence of suitable substrates. *Diraphora bellicostata* and *A. gregaria* are predominantly preserved attached to *P. muricata* in the Walcott Quarry Shale Member. Both *D. bellicostata* and *A. gregaria* are conspicuously absent in the younger Raymond Quarry Shale Member where *P. muricata* is also absent. Four specimens of *A. gregaria* are attached to a *C. eros* specimen, however, *C. eros* is extremely rare in the Raymond Quarry Shale Member (Bengtson and Collins, 2015). Both *A. spinosa* and *L. waptaensis* have been interpreted as potentially anchoring to substrates covered by the cyanobacterium *Morania* (Walcott, 1919; Holmer and Caron, 2006; Pettersson Stolk et al., 2010) and their respective absences from the younger Raymond Quarry could be correlated with the disappearance of *Morania* from the younger strata. If *D. bellicostata*, *A. gregaria*, *A. spinosa*, and *L. waptaensis* were specialized in settling and attaching to a particular substrate, then their distribution and ability to thrive in an environment was controlled entirely by the presence of that particular substrate.

Conversely, *Micomitra burgessensis* and *Nisusia burgessensis* both exhibit the ability to attach to a variety of substrates (Fig. 6). Despite being predominately attached to *P. muricata* in the Walcott Quarry Shale Member, *Micomitra burgessensis* dominates the Raymond Quarry community where *P. muricata* is absent, and also represents the species of brachiopod in the Burgess Shale with the widest variety of substrate attachments (Fig. 6).

It is thus conceivable that the distribution of brachiopods in the “thick” Stephen Formation is intricately linked with the presence or absence of particular benthic organisms that were preferred substrates for attachment. A simplistic explanation would be that the specialized attachment strategies of *D. bellicostata*, *A. gregaria*, *A. spinosa*, and *L. waptaensis* and the subsequent disappearance of their chosen substrate (*P. muricata*, *Morania*, and near disappearance of *C. eros*) resulted in their decline and ultimate absence from younger strata. Other species, notably *M. burgessensis*, exhibit a more generalist approach to settlement and attachment. The disappearance of relevant substrate taxa and their associated specialist brachiopod epibionts resulted in a homogenized community in the Raymond Quarry Shale Member, dominated by a single taxon, *M. burgessensis*.

Despite our interpretation of *Micomitra burgessensis* as an attachment generalist, this taxon overwhelmingly favoured attachment to *P. muricata* in the Walcott Quarry Shale Member. Attachment exclusions may have been due to the character traits of the host, as in the case of the spicules of *Takakkawia lineata* Walcott, 1920 and *H. palmata*, that were most likely covered by soft tissue in life and difficult for brachiopod larvae to attach to (Rigby et al., 1997; Rigby and Collins, 2004; Botting et al., 2012). The spicules of *P. muricata* projected from the sponge body wall and are not covered by soft tissue (Botting, 2007; Topper et al., 2015; figs

2-4, 8), most likely representing a stable attachment site. The absence of projecting spicules does not explain all cases, however. Potential substrate organisms possessing long spicules like *P. muricata* that would be suitable for brachiopod attachment, such as *Halichrondites elisa* Walcott, 1920 and *Choia carteri* Walcott, 1920, have no attached epibionts. The high frequency of *P. muricata* attachment also cannot be attributed to a lack of available host individuals. Despite showing a positive probabilistic species co-occurrence with a range of potential attachment options (such as *Tubulella* sp., *Chancelloria* sp., and *Vauxia* spp. - Supplementary Data 1.1), the overwhelming number of *M. burgessensis* settled and grew on *P. muricata* individuals, even in sample horizons where *P. muricata* specimens are rare (Supplementary Data 1.1). This would seem to indicate that the larvae of *M. burgessensis* may have possessed at least some degree of selectivity when searching for a suitable settlement and attachment point and preferred *P. muricata* as a substrate, unless that taxon was entirely absent.

Preferential settlements of extant brachiopod larvae on particular substrates have been experimentally proven in laboratory conditions (Pennington et al., 1999; their fig. 6). Brachiopod larvae have been observed seemingly ‘searching’ and ‘tasting’ potential sites before settlement (Pennington et al., 1999). The brachiopod larvae press their apical lobe against the substrate and can either attach on sites that the larvae deem appropriate or move onto an alternative substrate (Pennington et al., 1999). Settlement-inducing chemical cues have been suggested for brachiopods (Percival, 1960; Pennington et al., 1999; Peck et al., 2001), however, only a handful of investigations have been undertaken and the cues remain unknown. Other aspects of the attachment strategies of brachiopods in the Burgess Shale communities are also analogous to many extant brachiopod species (Fig. 7). Living brachiopod species, for

example, also tend to display a conspecific, gregarious behaviour, predominantly observed in shallow water habitats, as a mechanism to exclude competitors and grazers (Percival, 1960; Thayer, 1975; Noble et al., 1976; Noble and Logan, 1981; LaBarbera, 1985; Peck et al., 2001; Fig. 7D), and on muddy substrates (Pennington et al., 1999; Fig. 7A-B), presumably a consequence of the limited availability of hard substrates. Brachiopod larvae have been commonly documented settling near or on conspecific shells, frequently on the anterior edge of the maternal shell, leading to the formation of dense, grape-like clumps of brachiopods (Doherty, 1979; Thayer, 1981; Pennington et al., 1999; Peck et al., 2001; Mergl, 2010; Fig. 7A-B). Settling on the anterior edge of the maternal shell not only provides a secure attachment point, but would also reduce the amount of time the larvae has to spend suspended in the water column searching for a suitable hard substrate, reducing predation risk. The conspecific, gregarious attachment strategies of extant brachiopod species and Burgess Shale taxa, most notably *M. burgessensis*, appear to have changed little since the phylum first evolved in the Cambrian.

5.2 Primary and secondary tierers: a collaborative existence

We find no evidence to suggest that Burgess Shale brachiopods were concentrated at a specific height on their host substrate. As the distribution of values for the ratio of brachiopod height to host maximum height cannot be distinguished from a uniform distribution, this means there is equal probability for all attachment heights on a host substrate. The increased frequency of individuals attached at 50% of substrate height (Fig. 13A) possibly reflects greater surface area around the middle of the host substrate, but our overall result does not suggest preferentiality. The

brachiopod presumably just attached at the first point of suitable contact. Secondary tiering was therefore not a mechanism to provide brachiopod epibionts with maximum distance from the sediment-water interface. If this were the case, we would expect the majority of brachiopod epibionts attached to the upper part of their host substrate and a greater frequency of values above 50% of host maximum height. These results are consistent with the way extant brachiopods attach to known biological substrates, where attachment occurs as soon as the selected site is appropriate for attachment (Pennington et al., 1999; Peck et al., 2001).

Previous work has attributed the development of tiering to the increased rate of predation and competition for nutrients in the Palaeozoic (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986). Predation on brachiopods in the Burgess Shale community has been investigated recently by Topper et al. (2015) who concluded that the low percentage of brachiopod valves documented in the gut contents of the priapulid worm *Ottoia prolifica* Walcott, 1911, (see Vannier, 2012) and the lack of evidence for duraphagous activity suggests that the rate of predation on brachiopods in the community was relatively low. This presents the possibility that brachiopods in the Burgess Shale did not occupy a greater range of tiering heights as a response to predation, as there was no ecological imperative to do so. The height of a suitable stable, host substrate was perhaps the only controlling factor. In the case of the Burgess Shale, this translates to the height of *P. muricata* as the primary limit on brachiopod tiering height.

Every brachiopod in the Burgess Shale presumably fed from the same general food resource, including living and/or dead particulate organic material suspended in the water column, as extant brachiopods do today (James et al., 1992). It would seem advantageous that a variety of niches would need to be established in order to support

the diversity of brachiopods (Hardin, 1960; Armstrong and McGehee, 1980; Amarasekare, 2003). There is also presumably a strong relationship between the tiering height of secondary tierers and the diversity and abundance of primary tierers present in the community. Secondary tierers need a point of attachment and consequently their tiering height is somewhat dependent on the substrate chosen to attain their position above the sediment-water interface. If only low primary tierers are present on the seafloor, then secondary tierers will not have the necessary ‘footholds’ to reach higher tiering levels, whilst the presence of high primary tierers in a community does not necessarily translate to high secondary tierers, as epibionts can attach at any point on the primary tierer.

Tall sponge taxa (> 200 mm height; Walcott, 1920; Rigby, 1986; Bengtson and Collins, 2015) frequently co-occur with brachiopods in the Walcott Quarry Shale Member (e.g., *Hazelia* and *Halichondrites*), yet the majority of brachiopods occupy a height of 16 mm or less (Fig. 10). Like substrate choice, this lack of brachiopods at greater tiering heights cannot be attributed to a lack of suitable host individuals. *Hazelia palmata* Walcott, 1920, for example, represents one of the most common species in the Walcott Quarry Shale Member (approximately 10% in total relative abundance; Caron and Jackson, 2008), frequently co-occurring with *M. burgessensis* and *N. burgessensis* individuals (Fig. 8J-K). It reaches heights of 150 mm (Rigby and Collins, 2004), yet only a single specimen of *N. burgessensis* is attached to *H. palmata* (ROM56248, Fig. 8J-K).

Pirania muricata, the primary substrate choice, is one of the smallest sponges (in terms of height) in the “thick” Stephen Formation. Individuals most commonly range from 14 mm to 25 mm in height and can reach a documented maximum height of 30 mm (Rigby, 1986; Rigby and Collins, 2004); however, the mean height of *P.*

muricata specimens examined herein with brachiopod individuals attached is 18 mm (Figs 2-4, 8). When *P. muricata* is absent, as in the Raymond Quarry Shale Member, a greater proportion of brachiopods exceed the apparent 16 mm ceiling. In the Walcott Quarry Shale Member, only 10% of specimens reach a tiering level above 16 mm, compared with 38% of tiered specimens in the Raymond Quarry Shale Member.

The processes controlling the positioning of brachiopod larval settlement on appropriate substrates is unclear. Our results support the interpretation that brachiopod larvae attached at the first point of contact, but the relatively even distribution of individuals on the same substrate (Fig. 8) implies that some form of positioning mechanism existed. An even distribution of individuals on a host substrate would potentially maximize the attachment area, ensuring minimal disruption to growth by other attached individuals. As demonstrated recently by Topper et al. (2015), the chaetae possessed by *M. burgessensis* and *P. zenobia* were potentially utilized as a buffer zone to dissuade brachiopod larvae from settling on or close to their shell. The lack of suitable hard substrate and aspects such as the chaetae-related deterrence of *M. burgessensis* and *P. zenobia* may have been responsible for the tiering organization evident in the Burgess Shale brachiopod communities, as brachiopod individuals looked to settle and attach in any suitable location that would enable unimpeded feeding and growth.

5.3 Cambrian comparisons

The other preeminent Cambrian deposit to preserve brachiopods in such an exceptional manner, giving us a window into their ecology and adaptive morphologies, is the Chengjiang Biota of Yunnan, China. The brachiopod community

from the middle Cambrian Kaili Biota of China, although more comparable in terms of age and faunal composition (Zhao et al., 2005), is bereft of soft-part preservation and with no specimens preserved with pedicle or attached to a substrate, a satisfactory ecological comparison is unachievable. The Chengjiang Biota represents an earlier slice of time (Cambrian Series 2, Stage 3), a different depositional environment (Chen and Erdtmann, 1991; Zhu et al., 2005; Zhao et al., 2013) and a disparate brachiopod assemblage (Zhang et al., 2004, 2006, 2007a, b, c, 2009, 2011; Zhang and Holmer, 2013; Wang et al., 2012, 2014). In terms of species diversity, the Burgess Shale brachiopod assemblage (7 species) is comparable to the Chengjiang brachiopod community (8 species). However, no species or even genera are common across both communities. The life strategies of the Chengjiang brachiopods are also extremely varied and in stark contrast to the Burgess Shale brachiopod communities. The majority of Chengjiang brachiopod species possessed long pedicles of variable width and either attached directly to the sediment or to skeletal debris (see Zhang and Holmer, 2013, for review).

Despite the abundance and diversity of sponges in the Chengjiang fauna (Wu et al., 2014), not a single brachiopod is preserved attached to a sponge.

Approximately eighteen sponge genera have been reported from the Chengjiang Lagerstätte, although *Pirania* is absent from the community (Wu et al., 2014). Instead, the lingulid *Diandongia pista* (Rong, 1974) is frequently utilized as a hard substrate (Zhang et al., 2006, 2007a), most likely a result of the high abundance of the species (nearly 2000 individuals documented) rather than a host-specific association. The large majority of Chengjiang brachiopod species are also classified as both low primary and secondary tierers, occupying the 50 mm interval above the sediment-water interface. The two exceptions are *Eoglossa chengjiangensis* (Jin, Hou and

Wang, 1993) that possesses a pedicle with a maximum length of 60 mm and is interpreted as attaching directly to the sediment (Wang et al., 2014) and the acrotretid *Kuangshanotreta malungensis* Wang, Zhang, Holmer, Hu, Wang and Li, 2012 with individuals perched approximately 55 mm above the substrate on the branching algae-like form, *Malongitubus kuangshanesis* Hu, 2005 (Wang et al., 2012).

Wang et al. (2012) postulated that the thin, short pedicle and small body size allowed acrotretoids to occupy a higher tiering level above the seafloor, an ecological niche that the larger, heavier-shelled brachiopods in the Chengjiang community could not inhabit. Wang et al. (2012) attributed this ability to attach at these higher tiering levels as a catalyst for the dramatic diversification that acrotretids experienced in the middle Cambrian. *Acrothyra gregaria* in the Walcott Quarry Shale Member is commonly associated with the filamentous cyanobacteria *Marpolia* Walcott, 1919 (see Conway Morris and Robison, 1988), frequently occurring on bedding planes amongst tangled masses of the cyanobacterium. Attachment is not obvious, however, it is plausible that the small size of *A. gregaria* permitted attachment to the cyanobacteria, in a similar strategy to that employed by *K. malungensis* in the Chengjiang Biota. However, of the attached *A. gregaria* specimens, with the exception of four individuals found on one *C. eros* specimen, all specimens occupy low tiering intervals. This does not lend much support to the hypothesis put forward by Wang et al. (2012) that acrotretids exploited the higher tiering intervals. There is a host of potential reasons for the differences in attachment and life strategies between the two brachiopod communities, but without detailed information on environmental conditions (which is still under debate for the Chengjiang fauna; see Zhao et al., 2013), and a taxonomically comparable brachiopod fauna, direct comparison is difficult. What is immediately evident from the two communities, though, is that by

the middle Cambrian (Series 3, Stage 5) a diverse assemblage of brachiopods had already developed a range of ecological strategies to interact with both the substrate and other organisms in the ecosystem.

6. Conclusions

Brachiopods were undoubtedly presented with many challenges on the soft, muddy Burgess Shale seafloor. Destabilized sediment and suspended sediment caused by weak bottom current and mobile benthic organisms could have easily buried and suffocated settling brachiopod larvae. The seafloor was not conducive for direct attachment and the need to settle and attach to a harder substrate in a fashion that would not impede feeding and growth was undoubtedly one of the primary constraints on their survival and distribution. Brachiopods therefore attached to a range of hard substrates, including skeletal debris, conspecific brachiopods and enigmatic tubes, but with an overwhelming preference for attachment on the sponge *P. muricata*. The ecological relationship with *P. muricata* that continued throughout the Walcott Quarry Shale Member would have provided brachiopods with a suitable attachment point, elevating the individual above the muddy seafloor and also reducing the chance of biofouling and incidental sedimentary disturbances. The dominance of *P. muricata* as a substrate choice, even in bedding assemblages where *P. muricata* individuals are rare, implies that brachiopod larvae may have had some control over in their area of settlement. A range of larger organisms, co-occurring with brachiopod taxa and potentially suitable for attachment, were not utilized, providing further evidence for selective settlement. Whether settlement-inducing chemical cues promoted settlement is unknown. This dependence on particular substrates may have been a limiting

ecological factor for the survival of some brachiopod species, as taxa that were more specialized and restricted to settlement on a particular organism declined in communities where their preferred substrate was absent. Such a hypothesis, however, would need additional fossil data from a number of sites to be explored further.

Brachiopods in the Burgess Shale did not contribute greatly to the overall maximum tiering height of the community. The large majority of brachiopods occupied a tiering interval within 16 mm above the sediment-water interface, with a maximum tiering height of 52.2 mm. Within this 16 mm interval, though, taxa exhibit a degree of tiering variability and are evenly distributed, demonstrating a balanced partition of vertical space. Although potentially selective over which substrate to permanently settle upon, once chosen, brachiopods larvae attached at the first point of contact with the elected substrate. The chaetae possessed by *M. burgessensis* and *P. zenobia* and the lack of available hard substrates may be responsible for this relatively evenly distributed tiering organization. Comparison with the brachiopod community of the Chengjiang Biota confirms that brachiopods were functionally diverse in their morphologies and life strategies. The view that brachiopods have contributed little to the tiering complexity (Ausich and Bottjer 1982; Bottjer and Ausich, 1986) of early marine ecosystems is not supported.

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Figure captions

Fig. 1. Relative abundance of brachiopod species in the (A) “thick” Stephen Formation and (B) Walcott Quarry Shale Member.

Fig. 2. *Micromitra burgessensis* Resser, 1938 from the ‘middle’ (Series 3, Stage 5) Cambrian “thick” Stephen Formation. (A-B) ROM63337.8 (same block at Fig. 3A), BW-155 cm. Plan view of individual attached to *Pirania muricata* (part and counterpart). (C-D) ROM57603, BW-120 cm. (C) Plan view of individual attached to an isolated *P. muricata* spicule. (D) Close-up of specimen posterior and attachment area. (E) ROM63180, WQ+30 cm, Plan view of individual attached to *P. muricata*. (F-G) ROM63187, BW-170 cm. (F) Plan view of individual attached to *P. muricata*. (G) Same specimen under polarized light. (H-I) ROM57602.1, BW-170 cm. (H) Plan view of individual attached to an isolated *P. muricata* spicule. (I) Close-up of specimen posterior and attachment area. (J) ROM63338, BW-130 cm, Plan view of individual attached to a fragment of *P. muricata* body wall. (K-L) ROM63339, RQ+8.4 m. (K) Close-up view of individual attached to *Vauxia gracilenta*. (L) Overall view of the same specimen. (M) ROM56952 BW-150 cm, Plan view of individual attached to a tergite fragment of an unidentified trilobite. (N) ROM63170, RQ+8.2, close-up of specimen posterior and attachment to *Tubulella* sp., scale bar 1 mm. (O) Overall view of the same specimen. (P) ROM63340, RT talus, Plan view of

ventral valve. (Q) ROM63341, RQ+8.4 m, Plan view of individual attached to *Allonnia tintinopsis*. All scale bars 5 mm unless otherwise stated.

Fig. 3. *Nisusia burgessensis* Walcott, 1924 from the ‘middle’ (Series 3, Stage 5) Cambrian “thick” Stephen Formation. (A-B) ROM63337.2 (same block at Fig. 2A), BW-155 cm. Plan view of individual attached to *Pirania muricata* (part and counterpart). (C) USNM66495, Phyllopod Bed, Plan view of individual attached (indicated by arrow) to the holotype specimen of *P. muricata*. (D) ROM57839.94, BW-150 cm, Plan view of individual attached to *P. muricata*. (E) USNM69690, Phyllopod Bed, Plan view of specimen showing dubious chaetae. (F) ROM57839.138, BW-150 cm, Plan view of individual attached to *P. muricata*. (G-H) ROM63342.2, BW-210 cm. (G) Plan view of individual attached to *P. muricata*. (H) Close-up view, scale bar 3 mm. (I) ROM63343.19, BW-210 cm, Plan view of individual attached to a tube of *Selkirkia columbia*. (J-K) ROM61116, BW-210 cm. (J) Close-up of individual attached to the dorsal spine of *Wiwaxia corrugata*, scale bar 1 mm. (K) Plan view of individual attached (indicated by arrow) to the dorsal spine of *W. corrugata*, scale bar 1 cm. (L-M) ROM63344, RQ+8.2 m. (L) Plan view of individual attached to *Allonnia tintinopsis*. Note two individuals of *Micromitra burgessensis* are present, one attached to *Vauxia gracilenta* (top left of image), *A. tintinopsis* is itself attached to a trilobite carapace, scale bar 1 cm. (M) Close-up of individual attached to *A. tintinopsis*. All scale bars 5 mm unless otherwise stated.

Fig. 4. Brachiopods from the ‘middle’ (Series 3, Stage 5) Cambrian “thick” Stephen Formation. (A-D) *Acrothyra gregaria* Walcott, 1924. (A-B) ROM57839.83, BW-150 cm. (A) Plan view of individual attached to *Pirania muricata*. (B) Same specimen

under polarized light. (C) ROM57839, BW-150 cm, Plan view of individual attached (indicated by arrow) to *P. muricata*. (D) ROM63345, BW-210 cm. Plan view of individual attached (indicated by arrow) to *P. muricata*. (E-J) *Paterina zenobia* (Walcott, 1924). (E-F) ROM63346, ST talus. (E) Plan view of conspecific cluster of individuals. (F) Close-up of individuals showing attachment area, scale bar 1 mm. (G-H) ROM63182, WT talus. (G) Plan view of individuals attached to a trilobite carapace. (H) Close-up of attachment area. (I) ROM63184, WT talus, Plan view of two individuals. (J), ROM63183, S7 Tulip Beds talus, plan view of individual attached to an unknown substrate. (K-L) *Diraphora bellicostata* (Walcott, 1924). (K) ROM63347, WT talus, Plan view of individual attached to *P. muricata*. (L) ROM63348, talus on Fossil Ridge, Plan view of *Diraphora bellicostata* and *Acrothyra gregaria* attached to *P. muricata*. All scale bars 5 mm unless otherwise stated.

Fig. 5. Elemental maps of brachiopods from the ‘middle’ (Series 3, Stage 5) Cambrian “thick” Stephen Formation. (A) ROM63169, RQ+8.2 m, *Micromitra burgessensis* with iron (dark blue), phosphorous (light blue) and calcium (green) mapped, width of left image 10.8 mm. Close-ups showing Ca+Fe and P to the right. (B) ROM63349.1, BW-170 cm, Interarea and delthyrial opening of *Nisusia burgessensis* with carbon (red) mapped and corresponding SEM image, width of image 1.5 mm. (C) ROM57603, WQ-120 cm, anteromedial chaetae of *M. burgessensis*, with carbon (red), phosphorous (light blue) and iron (dark blue) mapped and corresponding image below, width of image 6 mm. (D) ROM63185, Talus above Walcott Quarry, anteromedial chaetae of *Paterina zenobia*, with calcium (green), aluminum (yellow), silica (purple) and phosphorous (light blue) mapped and

corresponding SEM image, width of left image 2.7 mm. Close-ups showing Ca, P, Al in the middle and partial view of the same specimen under polarized light to the right.

Fig. 6. Abundance of brachiopod specimens preserved attached to a substrate, in the Walcott Quarry Shale Member (A), in the Raymond Quarry Shale Member (B), and across the “thick” Stephen Formation (C).

Fig. 7. Attachment strategies of extant brachiopods and brachiopods from the ‘middle’ (Series 3, Stage 5) Cambrian “thick” Stephen Formation. (A-B) *Laqueus californicus* (Koch in Chemnitz, 1848), Monterey Bay, California, collected from 500 m depth, SMNH142203. (A) Gregarious conspecific cluster of individuals, scale bar 3 cm. (B) Close-up of gregarious cluster of individuals attached on the shell of a larger individual (C) ROM63171, RQ+11.4 m, gregarious cluster of *Micromitra burgessensis* individuals, scale bar 5 mm. (D) *Discinisca lamellose* (Broderip, 1833), Namibia, NRM_PZBr141421, gregarious conspecific cluster of individuals attached on the shell of a larger individual. E) ROM63350, RQ+11.6 m, *Micromitra burgessensis* individual attached to the anterior edge of the maternal shell, scale bar 5 mm. (F) *Pictothyris* sp., Hiroshima, North Pacific Ocean, SMNH142205, two individuals attached to the tubular shell of a scaphopod. (G) ROM63170, RQ+8.2, *Micromitra burgessensis* individual attached to *Tubulella* sp., scale bar 5 mm. (H) *Terebratula vitrea* (Born, 1778), Naples, Mediterranean Sea, SMNH142202, two individuals attached to skeletal debris. (I) ROM63185, talus above Walcott Quarry, *Paterina zenobia* individuals attached to an unknown substrate, scale bar 5 mm. (J) *Liothyrella uva* (Borderip, 1833), south of Falkland Islands, South Atlantic Ocean, collected from 137-150 m depth, SMNH142204, individual attached to shell fragment.

(K) ROM63351, BW-260 cm, *Micromitra burgessensis* individual attached to a hyolith skeletal fragment, scale bar 5 mm. All scale bars 1 cm unless otherwise stated.

Fig. 8. Attached brachiopod specimens from the ‘middle’ (Series 3, Stage 5) Cambrian “thick” Stephen Formation. (A-E) ROM63352, BW-150 cm. Five brachiopod individuals attached to *Pirania muricata*. (A) Close-up of two individuals of *Nisusia burgessensis*, scale bar 1 mm. (B) Close-up of a *Micromitra burgessensis* individual, scale bar 1 mm. (C) Plan view of entire specimen. (D) Close-up of a *Nisusia burgessensis* individual, scale bar 1 mm. (E) Close-up of a *Acrothyra gregaria* individual, scale bar 1 mm. (F-G) ROM63353, BW-150 cm. (F) Plan view of two *Micromitra burgessensis* individuals attached to *P. muricata* and two *Nisusia burgessensis* individuals attached to another *P. muricata*. (G) Plan view of counterpart and in polarized light. (H-I) ROM57839.30-33, BW-150 cm. (H) Plan view of two *Micromitra burgessensis* individuals and a *Nisusia burgessensis* individual attached to *P. muricata*. (I) Close-up of individuals attached to *Pirania muricata*. (J-K) ROM56248, from a block correlated with 1 metre above the base of the Walcott Quarry. (J), Plan view of *Micromitra burgessensis* and *Acrothyra gregaria* attached to *P. muricata* with *Nisusia burgessensis* attached to *Hazelia* that is also attached to the *P. muricata* specimen and another *Micromitra burgessensis* attached to an isolated *P. muricata* spicule, scale bar 1 cm. (K) Close-up of *Micromitra burgessensis* and *Acrothyra gregaria* attached to *P. muricata*. (L) USNM59801, Phyllopod Bed, plan view of *Micromitra burgessensis* and *Acrothyra gregaria* attached to *P. muricata*. (M) ROM57839.123-125, BW-150 cm, Plan view of two *Nisusia burgessensis* individuals, *Micromitra burgessensis* and *Acrothyra*

gregaria attached to *P. muricata* (arrows assist in the location of attached specimens).

All scale bars 5 mm unless otherwise stated.

Fig. 9. Visualisation of tiering height measurements for two individuals of *Micromitra burgessensis* and a *Nisusia burgessensis*, ROM57839.30-33, BW-150 cm.

Fig. 10. Tiering heights for all attached brachiopods in the ‘middle’ (Series 3, Stage 5) Cambrian “thick” Stephen Formation, x-axis represents height above substrate and y-axis represents number of specimens. Note that for *Acrothyra gregaria* the highest tiering specimens are only included in the area chart.

Fig. 11. Tiering heights for all attached brachiopods in the ‘middle’ (Series 3, Stage 5) Cambrian Walcott Quarry Shale Member, x-axis represents height above substrate and y-axis represents number of specimens. Note that for *Acrothyra gregaria* the highest tiering specimens are only included in the area chart.

Fig. 12. Tiering heights for all attached brachiopods in the ‘middle’ (Series 3, Stage 5) Cambrian Raymond Quarry Shale Member, x-axis represents height above substrate and y-axis represents number of specimens. The single specimen of *Nisusia burgessensis* is only included in the stacked area chart.

Fig. 13. (A) Histogram and kernel density plot for $X = (\text{brachiopod height from substrate} / \text{host maximum height}) * 100$. For kernel density plot, $N = 79$; Bandwidth = 10.42. (B) Skewness-kurtosis plot for the ratio of brachiopod height to host maximum height, generated using the ‘fitdistrplus’ package (Delignette-Muller and Dutang,

2015) for R. List on bottom left is potential distributions. Bootstrap is non-parametric and uses 1000 replicates. Based upon observed value and associated bootstrap replicates, potential distributions are uniform, normal and beta.

Fig. 14. (A) Reconstruction of the Walcott Quarry Shale Member community. (B) Identification of species used in the community reconstructions. 1. *Micromitra burgessensis*; 2. *Nisusia burgessensis*; 3. *Acrothyra gregaria*; 4. *Diraphora bellicostata*; 5. *Lingulella waptaensis*; 6. *Acanthotretella spinosa*; 7. *Pirania muricata*; 8. *Hazelia conferta*; 9. *Chancelloria eros*; 10. *Takakkawia lineata*; 11. *Wiwaxia corrugata*; 12. *Scenella amii*; 13. *Haplophrentis carinatus*; 14. *Ottoia prolifica*; 15. *Canadia spinosa*; 16. *Tubulella* sp.; 17. *Olenoides serratus* and trilobite carapaces; 18. *Canadaspis perfecta*; 19. *Liangshanella burgessensis*; 20. *Marrella splendens*; 21. *Sidneyia inexpectans*; 22. *Anomalocaris Canadensis*. Animation by Phlesch Bubble via the Royal Ontario Museum and modified and compiled by Timothy Topper.

Figure 15. (A) Reconstruction of the Raymond Quarry community. (B) Identification of species used in the community reconstructions. 1. *Micromitra burgessensis*; 2. *Nisusia burgessensis*; 8. *Hazelia conferta*; 12. *Scenella amii*; 13. *Haplophrentis carinatus*; 14. *Ottoia prolifica*; 16. *Tubulella* sp.; 21. *Sidneyia inexpectans*; 22. *Anomalocaris canadensis*; 23. *Leandroia superlata*; 24. *Hurdia victoria*; 25. *Choia carteri*; 26. *Vauxia gracilenta*; 27. *Allonia tintinopsis*. Animation by Phlesch Bubble via the Royal Ontario Museum and modified and compiled by Timothy Topper.

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