



Evidence of sensory-driven behavior in the Ediacaran organism *Parvancorina*: Implications and autecological interpretations

Felicity J. Coutts^{a, b, *}, Corey J.A. Bradshaw^c, Diego C. García-Bellido^{a, b}, James G. Gehling^b

^a School of Biological Sciences, University of Adelaide, Adelaide, South Australia 5005, Australia

^b Earth Sciences Section, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia

^c School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia

ARTICLE INFO

Article history:

Received 22 May 2017

Received in revised form 31 August 2017

Accepted 24 October 2017

Available online xxx

Handling Editor: J.G. Meert

Keywords:

Ediacaran

Palaeoecology

Spatial aggregation

Parvancorina

Current alignment

ABSTRACT

The ancient in situ fossil seafloor communities of the Ediacara biota present an unparalleled window into the assembly of the earliest complex macroscopic organisms, including early animals on Earth ca. 555 million years ago (mya). The unique preservation style of Ediacara fossil seafloors preserves whole communities virtually ‘frozen in time’, including both living and dead organisms at the time of burial. This phenomenon, where the fossilized organisms are arranged as they were in life offers an unparalleled opportunity to examine ecological patterns in some of the earliest examples of animal communities in deep time. The small, anchor-shaped fossil genus *Parvancorina* is common among the Ediacara biota; however, its morphology and ecology have received little attention. Here, we describe a population of juvenile *Parvancorina* preserved on a section of fossil seafloor recently excavated from the characteristic Ediacara Member from Ediacara Conservation Park in the Flinders Ranges, South Australia. We applied spatial methods to the sample population of *Parvancorina* ($n = 202$) and found that they demonstrated two size-clusters, distinguishing juveniles from adults, and further analyses showed that the smaller specimens tended to be spatially aggregated. For the first time among any Ediacara taxon, we found that this sample population of *Parvancorina* demonstrated a strong bimodal orientation, suggesting that orientation played an important behavioral role in its autecology. The aggregated spatial distribution and bimodal orientation of *Parvancorina* likely resulted from behavioral responses to the influence of benthic currents, suggesting that *Parvancorina* had a complex sensory network, and was capable of motility.

© 2017.

1. Introduction

In the fossil record, there are few examples of clear spatial differentiation according to organism size, and these are largely either time-averaged assemblages of transported fossils or local accumulations of soft-bodied and shelly fossils (Kidwell, 1998). Unlike Ediacara seafloors, most other soft-bodied fossil assemblages are not in situ, and final orientations of specimens are largely a result of transportation immediately prior to or during burial. The observation of aggregation among living communities, whether they are benthic marine invertebrates or their terrestrial counterparts, can indicate complex behavior and ecological assembly rules, providing insight into processes such as reproduction (Brockmann, 1990; Speyer and Brett, 1985) nutrient exploitation (Olivier et al., 2000; Pawlik, 1992) and shelter-seeking (Dolan III and Butler IV, 2006; Vadas et al., 1986). Although preserved over half a billion years earlier, Ediacara fossil seafloor communities provide the most complete and accurate representation of the oldest complex organisms living on the seafloor at the time; thus, spatial analysis of these exceptionally preserved com-

munities could reveal significant implications for our knowledge of early animal life.

The Ediacaran fossil *Parvancorina* is a small, anchor-shaped fossil displaying apparent bilateral symmetry, antero-posterior differentiation (Fig. 2), and has been interpreted as a benthic marine animal with arthropod affinities (Gehling, 1991; Laflamme et al., 2013; Lin et al., 2006; Sperling and Vinther, 2010). While it has been compared with Cambrian arthropods such as *Skania* (Gehling, 1991; Glaessner, 1980; Lin et al., 2006) and *Primicaris* (Zhang et al., 2003), recent revisions of morphologically similar Cambrian arthropods disagree (Legg, 2015), so the phylogeny of *Parvancorina* is far from settled. Two species have been described: *Parvancorina minchami* (Glaessner, 1959) is known from both the Flinders Ranges of South Australia and the White Sea region of northwestern Russia. *Parvancorina sagitta* (Ivantsov et al., 2004) however, is so far described only from the White Sea localities (Naimark and Ivantsov, 2009). Individuals of the genus *Parvancorina* generally range between 1 and 40 mm in length and are known from dorsal external molds on the soles of siliciclastic beds (Naimark and Ivantsov, 2009). The main dorsal anatomy of *Parvancorina* consists of an anterolateral ridge intersected sagittally by a medial ridge (Glaessner, 1980) (Fig. 1), and based on their (apparent) consistent morphology from juveniles to adults they have been described as probable direct developers, implying that they were mobile throughout post-embryonic growth (Lin et

* Corresponding author at: School of Biological Sciences, University of Adelaide, Adelaide, South Australia 5005, Australia.

Email address: felicity.coutts@adelaide.edu.au (F.J. Coutts)

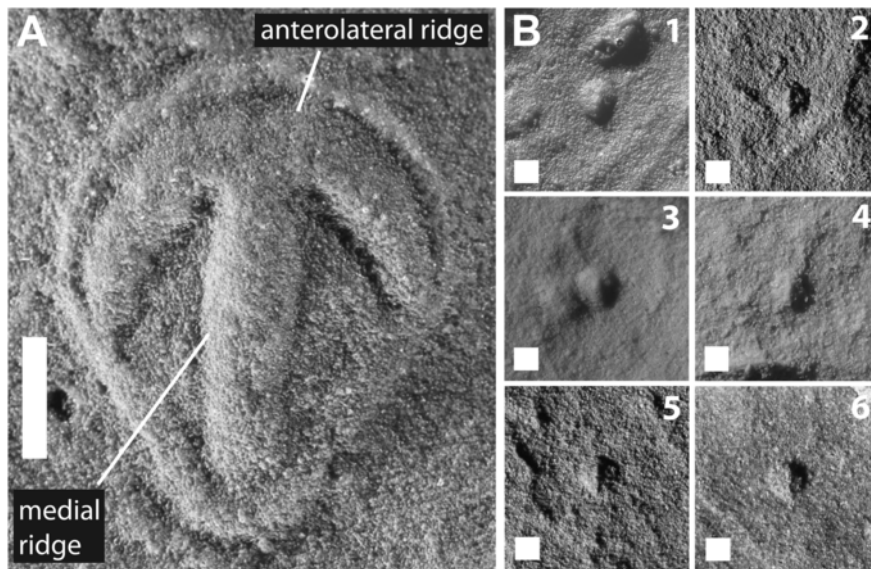


Fig. 1. Juvenile *Parvancorina* had a more pronounced medial ridge. A. Largest specimen of *Parvancorina minchami* on North Ediacara Conservation Park (NECP) Bed-1, SAM P49380 (South Australian Museum specimen identification number); B. Juvenile *Parvancorina minchami* observed on NECP Bed-1 and float slabs FK-1, FK-2 and FK-5 (not illustrated in Fig. 5). From top left: SAM P54500, SAM P54501, SAM P54502, SAM P54503, SAM P54504 and SAM P54505. Notice greater definition in the medial ridge relative to the anterolateral ridge of the juveniles, compared with the adult specimen. Scale bars: A: 5 mm; B(1–6): 1 mm.

al., 2006). However, the attribution of mobility, or any other informative ecological traits, when the only evidence of its existence are shallow concave impressions in siliciclastic beds, becomes problematic; thus, new applications for interpreting these fossils (e.g., spatial analyses) are necessary and may prove potentially revolutionary. In the Flinders Ranges, *Parvancorina* are usually observed as individuals or as small groups of individuals on fossil surfaces, with the exception of a single bed, called ‘Parv Bed’, at the National Heritage Listed fossil site Nilpena (Fig. 2A) hosting a population of ~ 100 intermediate-sized specimens (median length \approx 7 mm) (Droser, 2007; Paterson et al., 2017). Paterson et al. (2017) recently demonstrated a unimodal orientation in the population of *Parvancorina* on the Parv Bed, providing sufficient evidence to suggest that *Parvancorina* was capable of actively orienting itself as a response to benthic currents, at some stage during its life cycle.

Here, we report the preservation of a dense population of juvenile *Parvancorina* (most of which < 2.5 mm in length) on a section of fossil seafloor (NECP Bed-1) 1.6 m² in surface area and ten smaller non-contiguous ‘float slabs’ from the northern region of Ediacara Conservation Park (NECP) (Fig. 2A). We investigate for the first time the spatial distribution of a population of *Parvancorina*, as well as their orientations, and propose that if the organism represented archaic ancestors of living phyla, or displayed evidence of behavior that would suggest they were motile bilaterians, this should be evident in their spatial autecologies. Specifically, we hypothesize that: 1. There is evidence of different size classes of *Parvancorina* based on specimen length, and that this distinguishes ‘juvenile’ *Parvancorina* from ‘adults’. 2. If hypothesis 1 is supported, different size classes (e.g., juveniles vs. adults) demonstrated different morphologies of the anterolateral and medial ridge. 3. Difference in anterolateral and medial ridge morphology between size classes imparted different drag in benthic water currents. For example, the orientation of specimens with a more pronounced medial ridge and reduced anterolateral ridge would be more vulnerable to the influence of benthic currents. 4. If hypothesis 3 is supported, higher dependency of orientation on dominant water current should lead to higher spatial aggregation.

2. Sedimentary setting

The Ediacara Member sits within the Pound Subgroup in the faulted and folded sediments of the Flinders Ranges (Fig. 2) and contains packages of fossilized siliciclastic seafloors that record benthic marine Ediacaran communities in situ. The Ediacara Member is exposed in many locations within the strata and is characterized by wave- and current-rippled tops with iron oxide-stained soles, which preserve Ediacara body and trace fossils among microbial- or algal-induced textured organic surfaces (Gehling and Droser, 2009). > 555 million years ago the sediments that now comprise the Flinders Ranges were deposited within a north-northwest to south-southeast trough, with a shoreline to the west and a depositional high in the form of the Curnamona shelf to the east of the ranges. Storms reworked deltas on the basin margins, sending sand downslope to smother seafloor communities established below fair-weather wave-base and out over delta fronts. Frondose and other larger organisms, on seafloors near fair-weather wave-base, were torn out and transported offshore into deeper water channels and canyons (Tarhan et al., 2010; Tarhan et al., 2015).

The Ediacara Member in the north of Ediacara Conservation Park (northwestern margin of the Flinders Ranges) records a package of fine-grained fossiliferous seafloors. The Ediacara sequence displays a thickening and coarsening upwards of depositional event beds. Fossil horizons consist of ferruginous, fine-grained and thin siliciclastic beds (between 2.5 and 4 cm thick), bearing low-angle current-ripple tops, and reflect a submarine delta-front sand facies. Bed bases mold well-developed textured organic surfaces that are irregular in pattern and texture. The fine-grain size and ferruginous coatings of sand in these beds suggest limited wave reworking and deposition (below storm wave-base) than the coarser grains and better-sorted rippled beds deposited above the storm wave-base in the Ediacara Member. The facies consists of fine- to medium-grained sandstone (< 100–500 μ m) with rarer large sand grains and ferruginous, millimeter-thick silt, to fine-grained sand partings between more coherent sandstone beds.

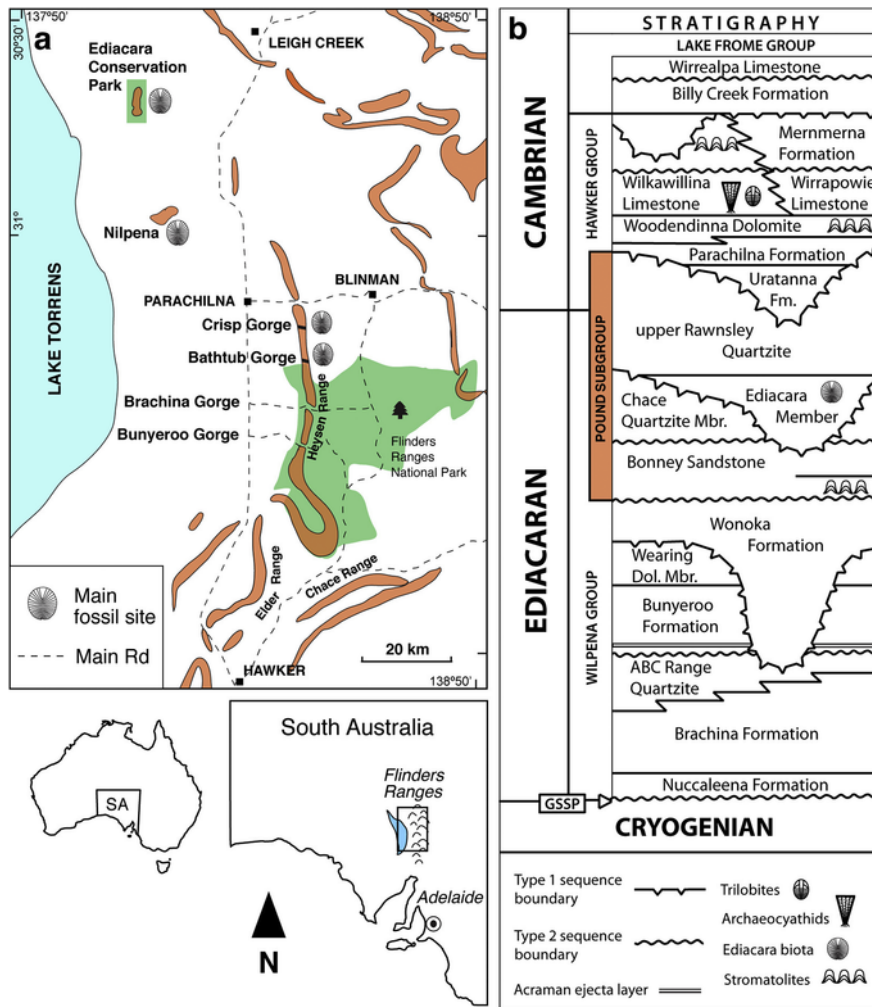


Fig. 2. Fossiliferous Ediacaran outcrop in the Flinders Ranges, South Australia. A. Map highlighting (orange) the outcrop of the Pound Subgroup containing the fossil-bearing Ediacara Member in the Flinders Ranges, South Australia. B. Generalized stratigraphic succession of the Cryogenian-Ediacaran-Cambrian depositional sequences of the Flinders Ranges, showing the relative position of the fossiliferous Ediacara Member. For further description see SI Experimental Procedures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) *Figure modified from Coutts et al. (2016).*

Fossil communities preserved at the north Ediacara Conservation Park delta-front sand facies are diverse and include fossil impressions of low-lying sessile suspension-feeders, tall frondose forms such as *Charniodiscus*, and possible bilaterian-grade organisms such as *Dickinsonia* (Gold et al., 2015), *Spriggina* (Glaessner, 1958) and *Parvancorina* (Glaessner, 1958) (Coutts et al., 2016). *Parvancorina* is found in many submarine preservational environments within the Ediacara Member, including the wave-base, delta-front and sheet-flow submarine environments (Gehling and Droser, 2013), which are interpreted to indicate an increase in marine depth, respectively. No *Parvancorina* fossils have yet been recorded from the more energetic, shallower shoreface sands or the inundating mass-flow sands deposited in deeper settings.

3. Materials and methods

3.1. Collection and preparation of the fossiliferous material

After locating the source of slabs bearing type species of the Ediacara biota collected 40 years ago at north Ediacara Conservation

Park (Fig. 1A) about 150 m north-northwest of Greenwood Cliff (lower Cambrian deposits), amalgamation of partly outcropping slabs with excavated material resulted in a contiguous sample with a surface area of 1.6 m² (North Ediacara Conservation Park Bed-1: 'NECP Bed-1') (Coutts et al., 2016). Many non-contiguous fossil-bearing sandstone slabs with similar bed characteristics and textured organic surfaces were identified as being from the same package of fossil beds, and clearly represented the same horizon (Coutts et al., 2016). Selection of the fossil slabs to be collected was based only on the size, texture and thickness of the fragment, with careful consideration that it matched the characteristics of NECP Bed-1, and not the fossil impression content of the rock. Thin sand and silt laminae, adhering to the sole of NECP Bed-1 and other collected slabs, were removed with the use of vibro-tools to expose the silicified and ferruginized external molds preserved on the sole of overlying sandstone bed, without damage to that surface. The removed 'shims', that represent the mineralized remains of the colonized seafloor, originally preserved the positive, counterpart casts of external molds on NECP Bed-1 and accompanying sandstone bed samples (Gehling, 1999).

3.2. Data collection

To study these molded samples of benthic Ediacara communities, we cast the complete sole surface of each bed sample by application of 10 to 14 layers of black rubber latex and reinforced it with gauze for structural rigidity. We identified *Parvancorina* on the surfaces by their characteristic medial ridge and anterolateral ridge, and calculated the spatial distributions of *Parvancorina* by overlaying a 10×10 cm grid with millimetric indication onto the target surfaces, recording the position of *Parvancorina* (based on the center of each specimen) and creating a planar Cartesian coordinate system. Once measured, we uploaded the specific locations of specimens and their position coordinates into the R programming language (Team, 2015). We recorded *Parvancorina* length, lateral width (both in mm) and bearings using the medial ridge and the anterolateral ridge to orient each specimen (Fig. 1). Orientation was recorded using the widest end of the fossil. We excluded all specimens where we could not easily identify the anterolateral ridge or where we could not determine the wider end of the fossil (regarded as ‘anterior’) from the narrower end (regarded as ‘posterior’) (Glaessner, 1980).

To analyze the population structure of *Parvancorina*, it was first necessary to examine and quantify their growth patterns. To investigate our first hypothesis, we constructed growth trajectories based on the length and width data measured using digital Vernier calipers, which we frequently tarred to minimize drift.

3.3. Size class analysis

We determined evidence of size-class clusters of *Parvancorina* from the combined surfaces of NECP Bed-1 based on a maximum-likelihood method assessed using the Bayesian information criterion (BIC) implemented in the R package *mclust* (Fraley and Raftery, 2002; Fraley et al., 2012). We also log-transformed the measurements to estimate the size distributions (Meesters et al., 2001; Rolf and Erik, 1998).

3.4. Morphology, orientation and spatial distribution

To test our second hypothesis, we observed the preserved morphology of many juvenile and adult specimens collected from North Ediacara Conservation Park. To test our third hypothesis, we recorded the orientations of all the specimens on NECP Bed-1 and the float slabs, from which we created rose diagrams computed using the R package *ggplot2* (Wickham, 2009). We tested our fourth hypothesis by assessing the community on NECP Bed-1 for any trends in spatial distribution. For this we used the R package *spatstat* (Baddeley et al., 2015), which gives a planar point pattern and includes a two-dimensional plot showing the polygonal outlines of the rock, the relative positions of the individuals on that surface, and the area of the fossil surface (m^2). Having produced the planar point pattern, we applied the following three functions to the model to investigate the presence of spatial clustering and associations between spatial distribution, size and specimen orientation. First, we used the nearest neighbor cluster analysis tool, *G* Function, to identify the presence of clustering. The *G* function $G(r)$, where r = distance (cm), assumes that a point process is stationary, and for any point in the pattern it defines the cumulative distribution function for that point by using the distance to its nearest neighbor (Baddeley et al., 2015). $\hat{G}_{observed}(r) > G_{Poisson}(r)$ indicates that nearest-neighbor distances in a point pattern (observed values) are closer together than that predicted by a Poisson process (theoretical values), and are therefore clustered.

$\hat{G}_{obs}(r) < G_{Pois}(r)$ indicates regularity, and $\hat{G}_{obs}(r) \approx G_{Pois}(r)$ indicates spatial randomness. We assessed spatial clustering for the entire sampled population of *Parvancorina* on NECP Bed-1, as well as among the defined size clusters from the BIC model to investigate clustering specific to *Parvancorina* size. We applied the ‘best’ edge correction option in *spatstat* to reduce bias in the cluster analyses.

To assess our fourth hypothesis, we tested for an association between specimen orientation and spatial distribution. We also applied a pair correlation function to the population to investigate the presence of paired specimens, where $\hat{g}(r) = 1$ corresponds to spatial randomness, and $\hat{g}(r) > 1$ indicates clustering (Baddeley, 2010). Finally, we used the function *markcorr* in *spatstat* to assess the presence of any association between inter-specimen distance and specimen size. We applied Monte Carlo envelopes with 999 simulations to all curves to analyze deviations from random.

4. Results

Specimens were more abundant on NECP Bed-1 ($n = 114$) than on the combined non-contiguous float slabs ($n = 88$) (Fig. 3A). The right-skewed length histograms produced were comparable between NECP Bed-1 and the non-contiguous surfaces (median *Parvancorina* length = 2.3 ± 1.72 and 2.4 ± 1.79 mm, respectively) (Fig. 3A), and show that the population was juvenile-dominated. Specimen length ranged from 1 to 16.4 mm, and included the smallest recorded specimen of *Parvancorina* (~ 1 mm) (Glaessner, 1980; Naimark and Ivantsov, 2009). Imprints of traces created by a larger Ediacaran organism (*Dickinsonia* sp.) were occupied by at least two juvenile *Parvancorina*, suggesting that the latter might have actively moved onto these traces after they were created (Coutts et al., 2016).

4.1. Two size classes are identified

We determined evidence for two size classes from *Parvancorina* length data of the combined fossil surfaces (Fig. 3B). This was based on a maximum-likelihood method assessed using the Bayesian information criterion (BIC) (see in text 2.3 and (Fraley and Raftery, 2002; Fraley et al., 2012). Of the two size classes demonstrated by the BIC top-ranked model (Fig. 3B), the first comprised a single population of smaller, ‘juvenile’ *Parvancorina*, and the second mostly larger or ‘adult’ specimens that shared a similar allometry to the first (see the bivariate classification regression plot in Fig. 3C). The first size class included abundant ($n = 159$), and small (length = 1 to 4 mm) specimens of ‘juvenile’ *Parvancorina*. The second size class was less abundant ($n = 22$) and included individuals of a broader range of sizes (length = 2 to 16.4 mm).

4.2. Morphological variation is observed

We found observable differences between the fossilized morphologies of the juvenile and adult specimens, where juveniles had a more pronounced medial ridge, and a relatively reduced anterolateral ridge compared to adults (see Fig. 1). The latter had both well-defined anterolateral and medial ridges.

4.3. *Parvancorina* specimens were bimodally oriented

On NECP Bed-1, the burial current direction is indicated by the orientation of the felled frondose fossil organism *Charniodiscus* (Coutts et al., 2016) (Fig. 4). The presence of an adjacent degraded frond, felled in a similar direction to the former specimen, suggests that a prevailing ambient current might have also had the same orien-

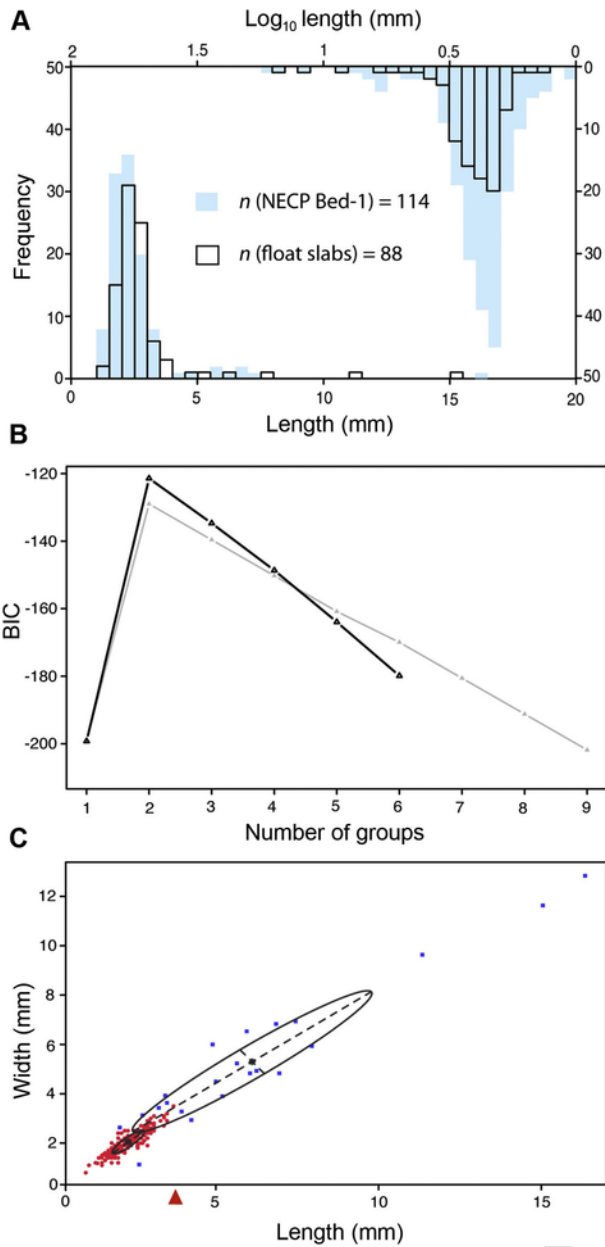


Fig. 3. NECP Bed-1 comprised a juvenile-dominated population, and two distinct size groups were present. A. Linear (bottom) and log-transformed (top) size frequency of length (in mm) of *Parvancorina* from North Ediacara Conservation Park (NECP) Bed-1 (blue fill, $n = 114$) and from the combined float slabs (black border, $n = 88$). Median *Parvancorina* length 2.3 ± 1.7 (SD) mm among specimens on NECP Bed-1 and 2.4 ± 1.8 (SD) mm among specimens on float slabs; B. Cluster analysis based on the Bayesian information criterion (BIC) supports the presence of two size classes among the logged measurements of *Parvancorina* specimens; C. Classification plot using unlogged measurements, showing the size ranges of the two size classes proposed. Red triangle indicates all specimens below 4 mm in length, distinct from those above 4 mm in length. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tation (Coutts et al., 2016). We therefore used this current direction as the null hypothesis for gauging orientations of *Parvancorina* on the fossil surface. The sample population of *Parvancorina* on NECP Bed-1 display a strong bimodal orientation, with approximately half of the individuals facing into the current direction and the other half away from the current direction (Coutts et al., 2016) (Fig. 4); furthermore, around 68% of specimens were aligned within 45° of the domi-

nant current direction compared with just 32% that were within 45° perpendicular to the current (Fig. 4). Therefore, most specimens appear to have their medial ridge aligned with the dominant current. The largest specimen on NECP Bed-1 appeared to be oriented almost perpendicular to the current direction (Fig. 6F). *Parvancorina* on nine out of the ten float slabs (illustrated in Fig. 4) also showed a dominant trend in orientation, although two of the float slabs had ≤ 2 specimens.

4.4. Juvenile *Parvancorina* were spatially clustered

The G function indicated that *Parvancorina* had an aggregated (i.e., non-random and non-uniform) distribution on NECP Bed-1 (Fig. 5A). Specimens were not abundant enough on the float slabs to show conclusive evidence of aggregation due to the small surface area of each slab (combined surface of all float slabs $\sim 1.5 \text{ m}^2$). Analysis by selectively testing for the aggregation of individuals among both the small-size class and the large-size class present on NECP Bed-1 demonstrated evidence that smaller individuals were aggregated (Fig. 5B), whereas larger specimens were not (Fig. 5C). We also tested for aggregation among the bimodal orientations, and found that *Parvancorina* with their wider ‘anterior’ ends pointing into the current and individuals with their narrower ‘posterior’ ends pointing away from the current demonstrated aggregation (Fig. 5E and F).

To test for aggregation between pairs of points, the pair-correlation function $g(r)$ of the population on NECP Bed-1 also indicated aggregation (Fig. 6a), and that no two individuals were farther than 5 cm apart. We found evidence for pair correlation at distances < 2 cm, consistent with the observation of paired individuals and the nearest-neighbor cluster analysis. Function *markcorr* did not identify any association between *Parvancorina* size and distance (Fig. 6b).

5. Discussion

5.1. Morphological variation and autecology

We found that *Parvancorina* on excavated surfaces from North Ediacara Conservation Park demonstrated two statistically distinguishable size classes. The first size class comprised a single population of smaller, ‘juvenile’ *Parvancorina*, while the second size class of larger specimens shared a similar allometry to the first. Thus, the two size classes observed satisfy our first hypothesis. The variation in length among the identified larger size class is too high to represent a single reproductive event (cohort). Therefore, we suggest that this mixed-size group of larger individuals independently moved onto this patch of seafloor in separate events to the single group of juvenile *Parvancorina*, and could have originated from one or more reproductive events.

We found reduced definition of the anterolateral ridge and more pronounced relief of the medial ridge among juvenile specimens compared to adults, which could conceivably arise from ontogenetic shifts in allometric growth during development. To attest to this observation, generally, smaller Ediacaran fossils tend to maintain a higher preserved relief compared with larger specimens, a phenomenon which is taphonomic, and could have resulted from of a combination of factors such as organism size, seafloor topography, flow velocity, sand grain size and various effects of directed compaction. Furthermore, since we find that small Ediacaran fossil organisms appear to be less distorted by the burial event, the morphology of the juveniles may demonstrate more accurately the dorsal morphology of

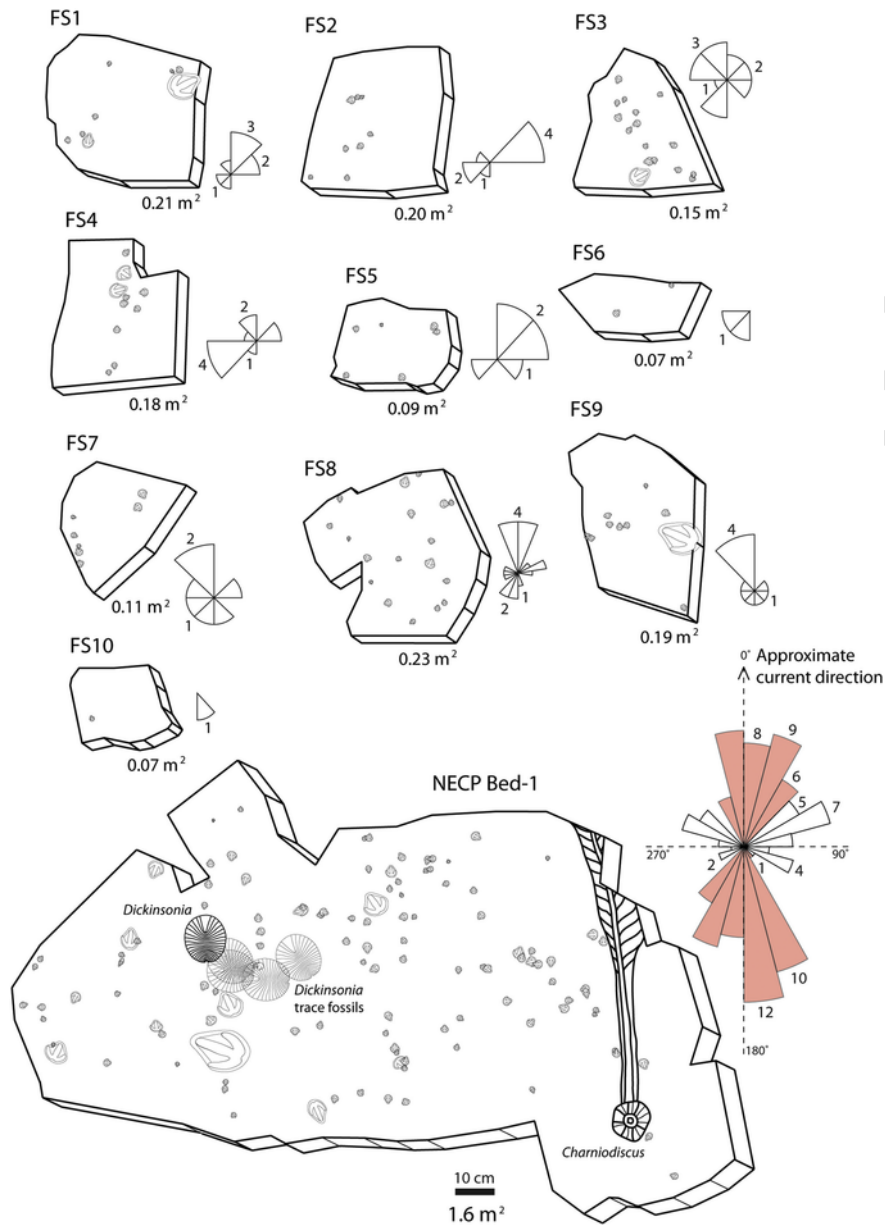


Fig. 4. Distribution of *Parvancorina* on the fossil seafloor. Spatial distribution of *Parvancorina* on North Ediacara Conservation Park (NECP) Bed-1 and float slabs, with relative orientations. The rose diagram of the specimens on NECP Bed-1 shows a strong bimodal bias in orientation (bottom right), where approximately 68% of all specimens are aligned within 45° of the current (shaded red), compared with just 32% of specimens oriented within 45° perpendicular to the current (white). Spatial distributions and orientations of *Parvancorina* on a sample of ten float slabs (above). All *Parvancorina* illustrated are proportionally larger than the rock slabs so that the smallest individuals are resolvable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Parvancorina, at that stage. The morphological differences observed between the two size classes therefore support our second hypothesis.

5.2. *Parvancorina* orientation

This is the first time a bimodal orientation has been described in *Parvancorina*, let alone for any described Ediacara taxon, where either unimodal trends (Droser, 2007; Liu et al., 2012; Paterson et al., 2017) or a lack of current-associated orientation have been described (Evans et al., 2015). The population of *Parvancorina* appeared to be aligned with the current, with no evidence of a method of attachment to the substratum. Recently, a study on the orientation patterns of ~ 100 intermediate-sized *Parvancorina* from the ‘Parv Bed’ in

Nilpena (Paterson et al., 2017) (for fossil site location see Fig. 2A) demonstrated a unimodal trend among the population. The minimum size of specimens in this population was about 3.5 mm, which is comparable to the largest specimens from our juvenile size class, and the median length of the population appears to be about 7 mm, which is close to three times the size of the average specimen in our study. This could suggest that bimodal orientations were more apparent in juvenile specimens. The medial ridge tended to be the most prominent dorsal feature in juvenile specimens, and this alone could be responsible for the difference observed in their bimodal orientations. It is plausible that the pronounced medial ridge, reduced anterolateral ridges and sub-rounded shape in smaller specimens would have made them more unstable if facing perpendicular to the current. Further, di-

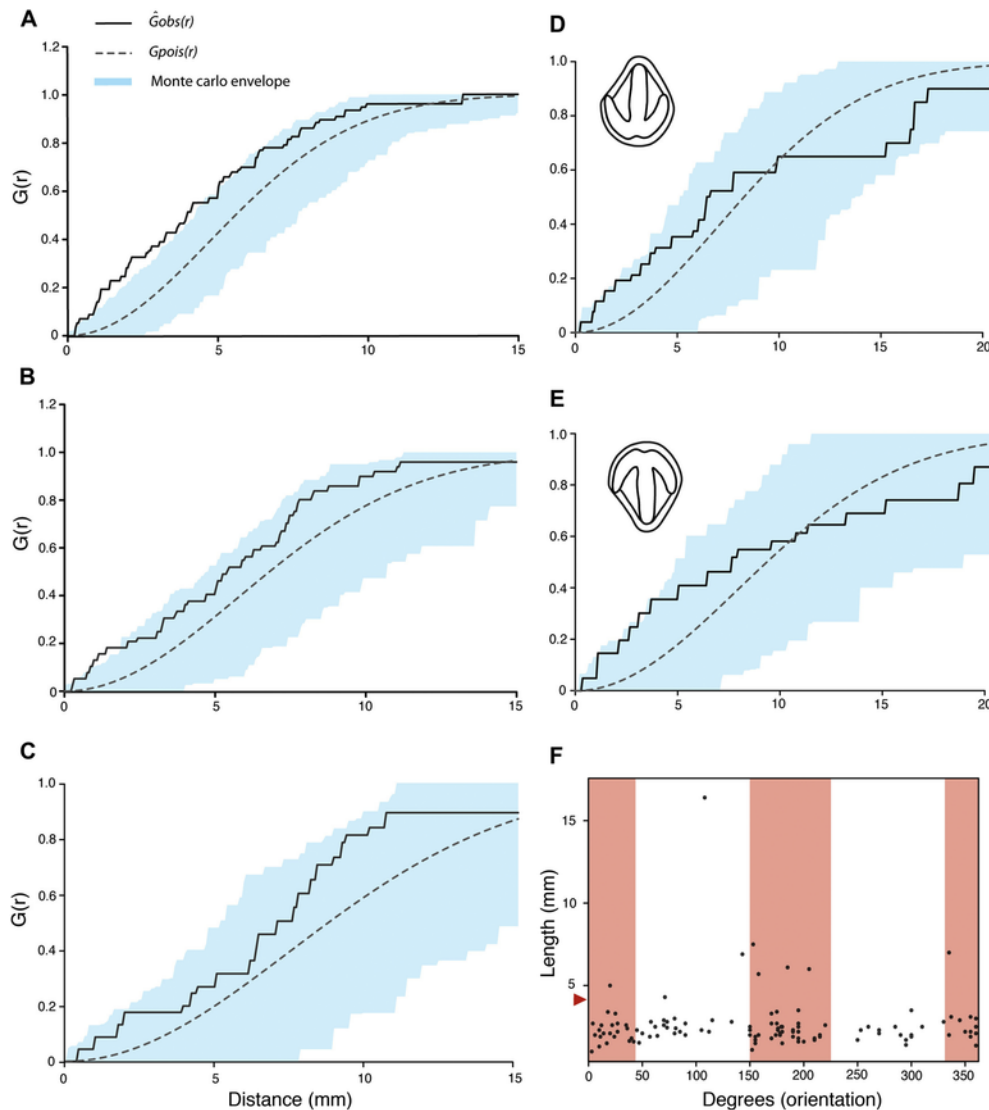


Fig. 5. Juvenile *Parvancorina* demonstrated spatial aggregation. A. Nearest-neighbor cluster analysis of *Parvancorina* on NECP Bed-1 shows that the specimens are spatially aggregated. Values of $\hat{G}_{obs}(r) > G_{Pois}(r)$ indicate a clustered spatial distribution while $\hat{G}_{obs}(r) \approx G_{Pois}(r)$ and $\hat{G}_{obs}(r) < G_{Pois}(r)$ indicate a random and regular spatial distribution respectively. We applied Monte Carlo envelopes using 999 simulations to all models (blue shaded area). Values of $\hat{G}_{obs}(r)$ above the Monte Carlo envelope indicate significant spatial aggregation; B. Cluster analysis of individuals smaller than the small-size cluster (demonstrated in Fig. 4B) show spatial clustering; C. Cluster analysis of the larger size class (Fig. 4B) do not show spatial clustering; D. Cluster analysis of specimens facing into the current show evidence of spatial clustering; E. Cluster analysis of specimens facing away from the current demonstrate evidence of spatial clustering; F. Scatterplot showing the orientation and length of all *Parvancorina* on NECP Bed-1. Red shaded areas envelope *Parvancorina* bimodally oriented within 45° of the current, as demonstrated in Fig. 5. Red triangle indicates specimens below 4 mm in length (first size group demonstrated in Fig. 4) distinct from those above 4 mm in length. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rectional movement in juveniles might have been more difficult than for adults and therefore alignment with the ambient current would have maximized stability. However, this conclusion requires further investigation into the hydrodynamics of *Parvancorina* morphology to determine the plausible effects that the current enforced on the dorsal morphology of the organism.

Given the evidence for two size classes displaying different morphologies, our data suggest that these differences imparted differential drag between the two groups, agreeing with our third hypothesis. Thus, the smaller size class of juveniles in the population on NECP Bed-1 appears to have depended more on the dominant water current than adults — larger specimens perhaps had more independent control over their orientations, whereas juveniles were more limited to axial alignment with the current direction owing to their reduced anterolateral ridge and comparatively pronounced medial ridge.

Behavioral taxis relative to currents is well documented across many marine invertebrate species to facilitate the search for food or shelter (Blair and Hedges, 2005; Budd and Jackson, 2016; Clapham et al., 2003; Fedonkin and Waggoner, 1997). Within the boundary layer of benthic currents, flow speed increases in a gradient from the almost stationary non-slip condition right up to the maximal flow speeds of the free-stream condition, which comprises the upper level of the prescribed boundary layer (Grasso and Basil, 2002; Vogel, 1994). The clear alignment of *Parvancorina* with the dominant current suggests that despite being low-lying organisms, the current affected their behavior enough such that they tended to align themselves with the flow.

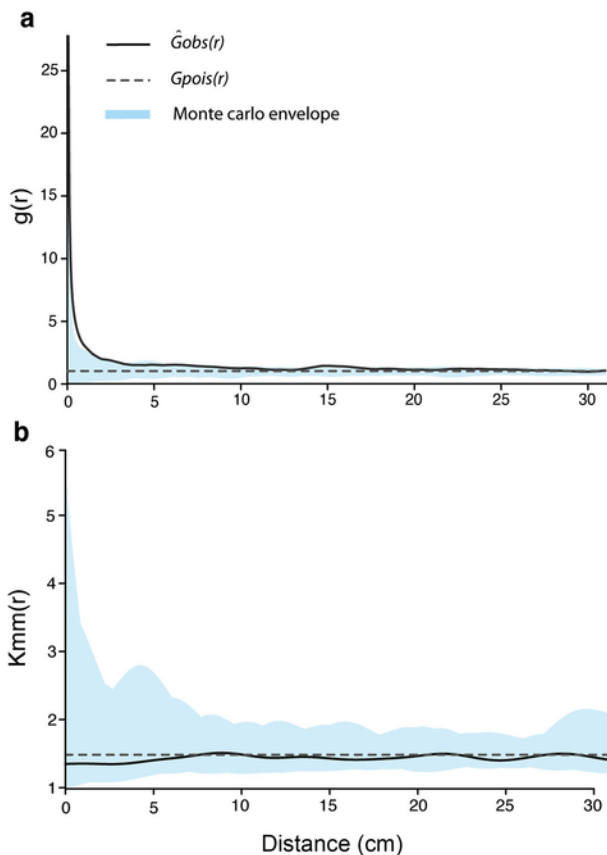


Fig. 6. Significant pairwise associations, no association between inter-specimen distance and size. a. Pair correlation function demonstrates evidence for pairwise associations. Values of $\hat{G}_{obs}(r) > G_{Pois}(r)$ indicate a clustered spatial distribution while $\hat{G}_{obs}(r) \approx G_{Pois}(r)$ and $\hat{G}_{obs}(r) < G_{Pois}(r)$ indicate a random and regular spatial distribution respectively. b. Lack of association between inter-specimen distance and size. Monte Carlo envelopes confidence envelopes (blue shaded areas) were calculated using 999 simulations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5.3. Spatial aggregation and autecology

Many fossil animal assemblages display spatial aggregation (Chatterton and Fortey, 2008; Weissburg, 2000), as well as many living marine organisms, including arthropods, foraminifera, gastropods, bivalves and polychaetes (Heip, 1975; Weissburg, 2000). In relatively primitive living phyla such as sponges, bryozoans and ascidians, larvae tend to settle near their mother, whether they are direct-developing or pelagic (Pawlik, 1992). This pattern of settlement is commonly referred to as a ‘Thomas process’, and describes the radially clustered spatial distribution of juveniles around a parent (Diggle et al., 1976; Thomas, 1949). This type of reproduction could be relatively archaic, as it has been described in a population of the older fusiform and reclining Ediacaran fossil *Fractofusus* (Mitchell et al., 2015), presumably a sessile organism. However, our population of juvenile *Parvancorina* preferentially cluster among themselves. Furthermore, patterns in aggregation are not only the result of settling larvae, studies have shown that juveniles are preferentially attracted to juvenile conspecifics (Dolan III and Butler IV, 2006; Nevitte et al., 2000; Pawlik, 1992).

The bias in paired distributions of *Parvancorina* (Fig. 6a) may imply a budding reproductive method. However, as a counter to this, the pairs are rarely observed touching and the size of individuals consti-

tuting the pairs are variable; i.e. not only do we observe large specimens alongside small specimens, but also small specimens alongside small specimens. Furthermore, if this was the case, we would surely see an obvious bias in size classes among the population structure. The possibility of budding is unlikely, as the only recorded living phyla that display this asexual reproductive method are the Cnidaria and Porifera, which lack key characters of bilateria; and Platyhelminthes (flatworms), which have an uncertain position within the bilateria (Madison and Schulz, 2007). Unlike sessile Ediacaran organisms such as the reclining fossil organism *Fractofusus* and the benthic attached fossil organism *Funisia*, *Parvancorina* display key characters analogous to animals, and are never observed overlapping one another. Instead, specimens appear to be independently, yet intimately associated within significant clusters.

The benthic region is an area of dynamic change in many living communities because it lies at the interface of fluid with the solid ocean floor (Grasso and Basil, 2002). In uninterrupted, planar substrata, viscous sub-layers can reportedly reach 6 mm above the sediment (Abelson and Denny, 1997); however, the topographically complex Ediacaran seafloor, created by microbial mat textures and protruding bodies such as *Charniodiscus* and natural undulations created by the lensing of sediment deposition and natural eddies, could have conceivably created heterogeneous patterns in benthic flow, with some areas having a relatively narrow boundary layer compared with others. *Parvancorina* could have aggregated within specific patches of seafloor which were less affected by strong or chaotic current flows. The juvenile *Parvancorina* observed in this study demonstrated a higher spatial aggregation than adults, supporting our fourth hypothesis. Thus, the spatial aggregation of juveniles could have been the responsive behavior of these organisms to benthic water currents.

Parvancorina were capable of living within a broad range of benthic submarine environments. Larger specimens have only been reported in small populations in diverse communities with the exception of a single bed at Nilpena (Droser, 2007; Paterson et al., 2017). As such, *Parvancorina* might have been efficient and active dispersers. Adults were possibly capable of moving to patches of seafloor away from their reproductive origins, which is likely the way in which the species was able to distribute itself over such broad submarine environments. Living species that display free-living pelagic larvae are capable of dispersing far greater distances than species that display direct-development; however, the distances for direct developers occur over the range of tens of kilometres (Yamada, 1989). Thus far, pelagic dispersal is described as the most commonly adopted dispersal method among the earlier frondose and fractal Ediacaran forms. This parallels the early onset of planktotrophy in the evolution of animal life (Pechenik, 1999), and to some extent explains the temporal and biogeographical scales at which some of these species dispersed. However, the apparent bilateral forms found in the Ediacara Member of the Flinders Ranges, notably *Parvancorina*, display comparably more conservative biogeographical ranges and constraints through time (Glaessner, 1958).

6. Conclusions

Our results demonstrate a strong correlation between the orientations, the presence of a pronounced medial ridge and spatial aggregation in a large population of juvenile *Parvancorina*. The prevalence of aggregating behavior is so apparent throughout the animal tree, including deep evolutionary time, it likely implicates core ecological benefits to the earliest communities on Earth. In addition to our observations of morphological differences between juveniles and adults,

the strong axial current alignment of juvenile specimens, regardless of whether they were facing into or away from the current, contrasts the unimodal orientations observed in larger specimens and apparently non-clustered spatial distributions (Paterson et al., 2017; see Supplementary information). Our findings strongly suggest that as the morphology of the anchor-shaped ridge changed with growth, this could have affected the way in which *Parvancorina* interacted with the surrounding benthic environment, and further that the development of *Parvancorina* was intimately entwined with its autecology. The responsive behaviors of aggregation and taxis demonstrate the potential complexity of these organisms, and suggest that even the earliest complex multicellular life must have had a sophisticated sensory network and specialized tissues that enabled them to move, sense, aggregate and interact with neighbors.

Uncited reference

Rahman et al., 2015

Acknowledgements

We thank the University of Adelaide and the South Australian Museum for access to literature and fossil material. We particularly thank M-A Binnie and J Bain of the South Australian Museum, as well as volunteers M Ellis, C Armstrong, J Perry, D Rice, F Peddie and J Light for fieldwork and fossil preparation. DCGB is supported by an Australian Research Council Future Fellowship (FT130101329).

References

- Abelson, A., Denny, M., 1997. Settlement of marine organisms in flow. *Annual Review of Ecology and Systematics* 28, 317–319.
- Baddeley, A., 2010. Analysing spatial point patterns in R. In: Workshop Notes. CSIRO online technical publication.
- Baddeley, A., Rubak, E., Turner, R., 2015. *Spatial Point Patterns: Methodology and Applications* with R. CRC Press, London.
- Blair, J.E., Hedges, S.B., 2005. Molecular phylogeny and divergence times of deuterostome animals. *Molecular Biology and Evolution* 22, 2275–2284.
- Brockmann, H.J., 1990. Mating behaviour of horseshoe crabs, *Limulus polyphemus*. *Behaviour* 114, 206–220.
- Budd, G.E., Jackson, I.S., 2016. Ecological innovations in the Cambrian and the origins of the crown group phyla. *Philosophical Transactions of the Royal Society, B: Biological Sciences* 371, 20150287.
- Chatterton, B.D.E., Fortey, R.A., 2008. Linear clusters of articulated trilobites from Lower Ordovician (Arenig) strata at Bini Tinzoulin, north of Zagora, southern Morocco. *Cuadernos del Museo Geominero* 9, 73–78.
- Clapham, M.E., Narbonne, G.M., Gehling, J.G., 2003. Paleocology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology* 29, 527–544.
- Coutts, F.J., Gehling, J.G., Garcia-Bellido, D.C., 2016. How diverse were early animal communities? An example from Ediacara Conservation Park, Flinders Ranges, South Australia. *Alcheringa* 40, 407–421.
- Diggle, P.J., Besag, J., Gleaves, J.T., 1976. Statistical analysis of spatial point patterns by means of distance methods. *Biometrics* 32, 659–667.
- Dolan III, T.W., Butler IV, M.J., 2006. The adaptive value of aggregation among juvenile Caribbean spiny lobster: an evaluation using individual-based modeling. *Journal of Crustacean Biology* 26, 565–578.
- Droser, M.L., 2007. Anchors away: anatomy of an Ediacaran sea floor dominated by *Parvancorina*. *Geological Society of America Bulletin* 39, 332.
- Evans, S.D., Droser, M.L., Gehling, J.G., 2015. Dickinsonia liftoff: evidence of current derived morphologies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 434, 28–33.
- Fedonkin, M.A., Waggoner, B.M., 1997. The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* 388, 868–871.
- Fraley, C., Raftery, A.E., 2002. Model-based clustering, discriminant analysis, and density estimation. *Journal of the American Statistical Association* 97, 611–631.
- Fraley, C., Raftery, A.E., Murphy, T.B., Scrucca, L., 2012. mclust Version 4 for R: Normal Mixture Modeling for Model-based Clustering, Classification, and Density Estimation, Technical Report. Department of Statistics, University of Washington.
- Gehling, J.G., 1991. The case for the Ediacaran fossil roots to the metazoan tree. *Memiors Geological Society of India* 181–223.
- Gehling, J.G., 1999. Microbial mats in the terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios* 14, 40–57.
- Gehling, J.G., Droser, M.L., 2009. Textured organic surfaces associated with the Ediacara biota in South Australia. *Earth-Science Reviews* 96, 196–206.
- Gehling, J.G., Droser, M.L., 2013. How well do fossil assemblages of the Ediacara Biota tell time?. *Geology* 41, 447–450.
- Glaessner, M.F., 1958. New fossils from the base of the Cambrian in South Australia. *Transactions of the Royal Society of South Australia* 81, 185–189.
- Glaessner, M.F., 1959. The geology and late Precambrian fauna of the Ediacara fossil reserve. *Records of the South Australian Museum* 13, 369–407.
- Glaessner, M.F., 1980. *Parvancorina* - an arthropod from the Late Precambrian (Ediacaran) of South Australia. *Records of the South Australian Museum* 13, 83–90.
- Gold, D.A., Runnegar, B., Gehling, J.G., Jacobs, D.K., 2015. Ancestral state reconstruction of ontogeny supports a bilaterian affinity for Dickinsonia. *Evolution and Development* 17, 315–324.
- Grasso, F.W., Basil, J.A., 2002. How lobsters, crayfishes, and crabs locate sources of odor: current perspectives and future directions. *Current Opinion in Neurobiology* 12, 721–727.
- Heip, C., 1975. On the significance of aggregation in some benthic marine invertebrates. In: *Ninth European Marine Biology Symposium*. pp. 527–538.
- Ivantsov, A.Y., Malakhovskaya, Y.E., Serezhnikova, E.A., 2004. Some problematic fossils from the Vendian of the southeastern White Sea Region. *Paleontological Journal* 38, 1–9.
- Kidwell, S.M., 1998. Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30, 977–995.
- Laflamme, M., Darroch, S.A.F., Tweedt, S.M., Peterson, K.J., Erwin, D.H., 2013. The end of the Ediacara biota: extinction, biotic replacement, or Cheshire Cat?. *Gondwana Research* 23, 558–573.
- Legg, D.A., 2015. The morphology and affinities of *Skania fragilis* (Arthropoda) from the middle Cambrian Burgess Shale. *Bulletin of Geosciences* 509–518.
- Lin, J.-P., Gon, S.M., Gehling, J.G., Babcock, L.E., Zhao, Y.-L., Zhang, X.-L., Hu, S.-X., Yuan, J.-L., Yu, M.-Y., Peng, J., 2006. A *Parvancorina*-like arthropod from the Cambrian of South China. *Historical Biology* 18, 33–45.
- Liu, A.G., McIlroy, D., Matthews, J.J., Brasier, M.D., 2012. A new assemblage of juvenile Ediacaran fronds from the Drook Formation, Newfoundland. *Journal of the Geological Society* 169, 395–403.
- Madison, R.D., Schulz, K.-S., 2007. In: Madison, R.D., Schulz, K.-S. (Eds.), *The Tree of Life Web Project*.
- Meesters, E., Hilterman, M., Kardinaal, E., Keetman, M., de Vries, M., Bak, R., 2001. Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. *Marine Ecology Progress Series* 209, 43–54.
- Mitchell, E.G., Kenchington, C.G., Liu, A.G., Matthews, J.J., Butterfield, N.J., 2015. Reconstructing the reproductive mode of an Ediacaran macro-organism. *Nature* 524, 343–346.
- Naimark, E.B., Ivantsov, A.Y., 2009. Growth variability in the late Vendian problematic *Parvancorina* Glaessner. *Paleontological Journal* 43, 12–18.
- Nevitte, G., Pentcheff, N.D., Lohmann, K.J., Zimmer-Faust, R.K., 2000. Den selection by spiny lobster *Panulirus argus*: testing attraction to conspecific odors in the field. *Marine Ecology Progress Series* 203, 225–231.
- Olivier, F., Tremblay, R., Bourget, E., Rittschof, D., 2000. Barnacle settlement: field experiments on the influence of larval supply, tidal level, biofilm quality and age on *Balanus amphitrite* cyprids. *Marine Ecology Progress Series* 199, 185–204.
- Paterson, J.R., Gehling, J.G., Droser, M.L., Bicknell, R.D., 2017. Rheotaxis in the Ediacaran epibenthic organism *Parvancorina* from South Australia. *Scientific Reports* 7, 45539.
- Pawlik, J.R., 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology. Annual Review* 30, 273–335.
- Pechenik, J.A., 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series* 177, 269–297.
- Rolf, P.M.B., Erik, H.M., 1998. Coral population structure: the hidden information of colony size-frequency distributions. *Marine Ecology Progress Series* 162, 301–306.
- Sperling, E.A., Vinther, J., 2010. A placozoan affinity for Dickinsonia and the evolution of late Proterozoic metazoan feeding modes. *Evolution and Development* 12, 201–209.
- Speyer, S.E., Brett, C.E., 1985. Clustered trilobite assemblages in the Middle Devonian Hamilton Group. *Lethaia* 18, 85–103.
- Tarhan, L.G., Droser, M.L., Gehling, J.G., 2010. Taphonomic controls on Ediacaran diversity: uncovering the holdfast origin of morphologically variable enigmatic structures. *Palaios* 25, 823–830.
- Tarhan, L.G., Droser, M.L., Gehling, J.G., 2015. Depositional and preservational environments of the Ediacara Member, Rawnsley Quartzite (South Australia): assessment of paleoenvironment proxies and the timing of ‘ferruginization’. *Palaeogeography, Palaeoclimatology, Palaeoecology* 434, 4–13.
- Team, R.C., 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

- Thomas, M., 1949. A generalization of Poisson's Binomial Limit for use in ecology. *Biometrika* 36, 18–25.
- Vadas, R.L., Elnor, R.W., Garwood, P.E., Babb, I.G., 1986. Experimental evaluation of aggregation behaviour in the sea urchin *Strongylocentrotus droebachiensis*. *Marine Biology* 90, 433–448.
- Vogel, S., 1994. *Life in Moving Fluids: The Physical Biology of Flow*, 2 ed. Princeton University Press, Princeton, New Jersey.
- Weissburg, M.J., 2000. The fluid dynamical context of chemosensory behaviour. *Biological Bulletin* 198, 188–202.
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Your Data Analysis*. Springer-Verlag, New York.
- Yamada, S.B., 1989. Are direct developers more locally adapted than planktonic developers?. *Marine Biology* 103, 403–411.
- Zhang, X.-L., Han, J., Zhang, Z.-F., Liu, H.-Q., Shu, D.-G., 2003. Reconsideration of the supposed naraoid larva from the early Cambrian Chengjiang Lagerstätte, South China. *Palaeontology* 46, 447–465.

UNCORRECTED PROOF