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Palaeoecology of Ediacaran communities from the Flinders Ranges of South Australia

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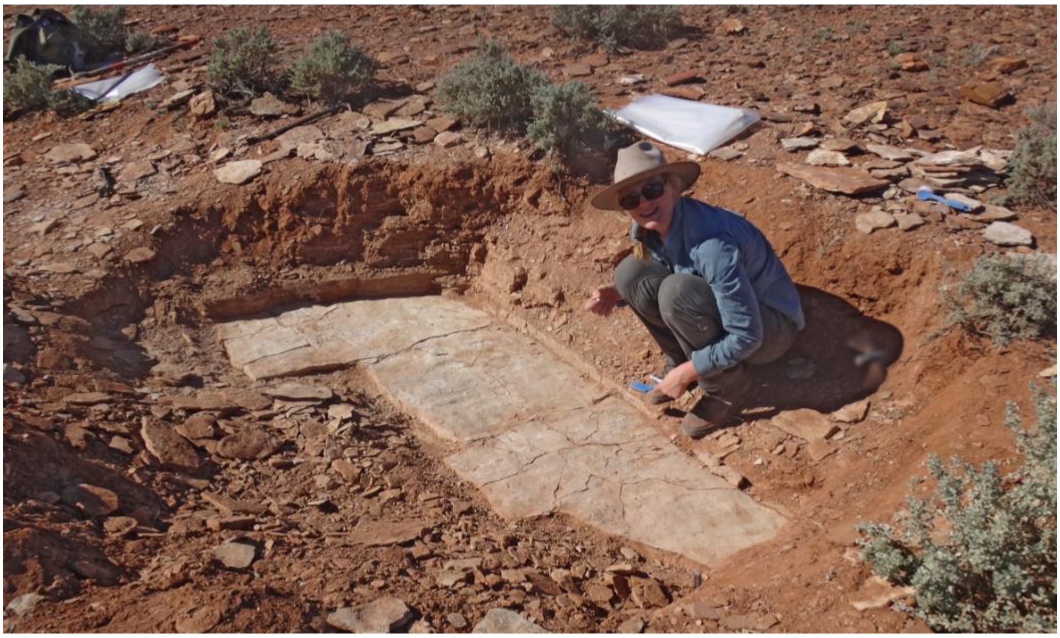
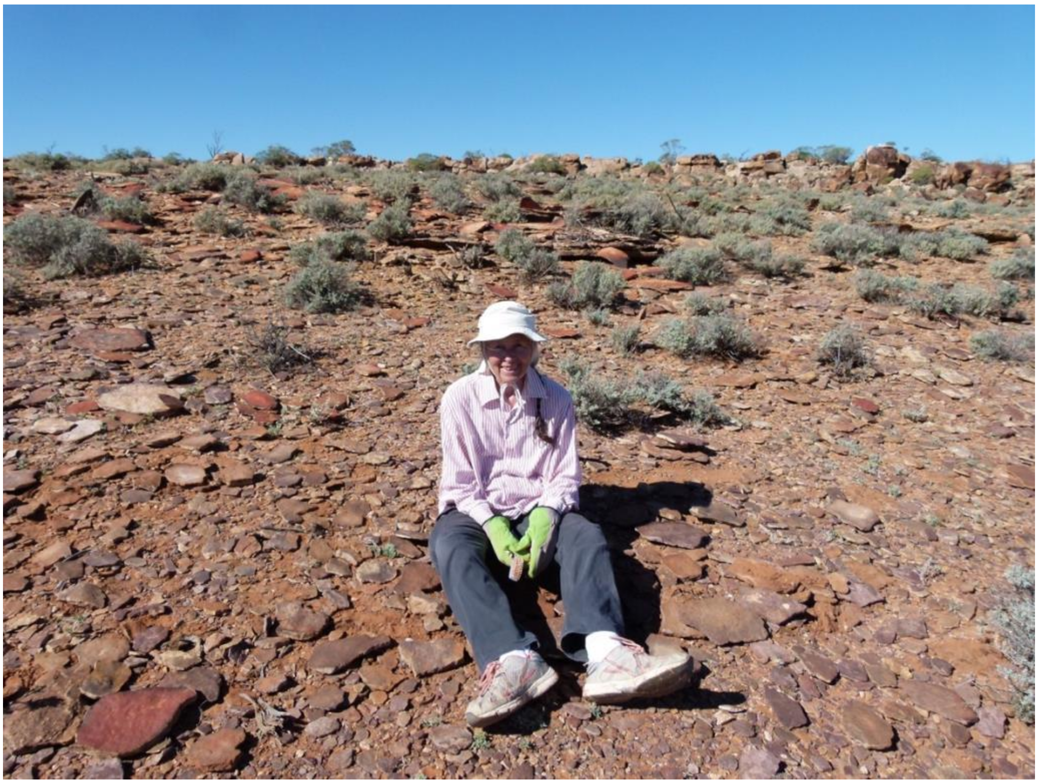
Doctor of Philosophy

This work was produced in collaboration with the School of Biological Sciences, University of Adelaide
and the South Australian Museum





In memory of Coralie Armstrong (1945–2017). She was an artist, nature-lover and an irreplaceable asset to Ediacaran palaeontology research at the South Australian Museum.

Contents

Abstract

If we could capture a glimpse of the earliest macroscopic communities on Earth, what might they have looked like? The globally distributed fossils of the Ediacara biota represent the earliest-known examples of multicellular life, and are our best chance of understanding how early macroscopic life evolved on Earth. The Ediacaran fossils of the Flinders Ranges in South Australia (~ 555 million years old) record ancient marine-benthic communities as shallow impressions in large expanses of stratified, fossilized seafloors. The unique preservation style of Ediacaran fossils, where largely external impressions replicate the locations of individuals on the ancient seafloor as they were in life (pre-burial and subsequent fossilization), allows for the analysis of inter- and intra-taxon spatial distributions and interpretation of organism behaviour. Furthermore, crude yet detailed impressions of the individuals allows for the limited analysis of morphological characters, and occasionally tentative placement within specific phyla. Due to limitations in preservation, the phylogenetic affinities of Ediacaran fossils are still debated. Assignments have ranged from extinct relatives of extant marine animals, to terrestrial fungi and lichens, to an extinct kingdom of life altogether. However, many palaeontologists today recognize Ediacaran fossils as a diverse collective of enigmatic marine organisms, some of which might represent the earliest examples of molluscs, cnidarians, echinoderms, sponges and arthropods.

The Flinders Ranges of South Australia preserves some of the world's most diverse Ediacaran communities, so Ediacaran seafloors from there have been the subject of many studies of Ediacaran palaeoecology. In my thesis I investigate the palaeoecology of select Ediacaran seafloors excavated from two main fossil sites from the western flanks of the Flinders Ranges: Ediacara Conservation Park and the National Heritage Listed fossil site in

Nilpena. Due to the high species diversity present on many Ediacaran seafloors, I explore the communities from a holistic perspective, comparing apparent ecological trends with living communities, as well as from a species-specific level.

The community ecology of a new fine-grained Ediacaran fossil bed recently discovered in Ediacara Conservation Park (NECP Bed-1) is explored. This fossil bed preserves a highly diverse community including dozens of specimens of the small enigmatic shield-shaped fossil *Parvancorina*, and two new undescribed genera. The diverse Ediacaran community, highly textured organic surface (TOS) and trace fossils are evident of successive events occurring on NECP Bed-1, and are indicative of a mature community at late-stage succession. Foremost, I focus on the small and relatively common shield-shaped fossil *Parvancorina*, which has been controversially interpreted as an early arthropod. Through nearest-neighbour cluster analyses of the *Parvancorina* population on NECP Bed-1 (*n* = 202), I demonstrate that two size-classes are present, distinguishing 'juveniles' from 'adults'. Furthermore, orientation analysis of the population showed a strong bimodal orientation in alignment with benthic currents, suggesting that orientation played an important role in its autecology.

Globally, there are two described species of *Parvancorina* inferred from traditional bivariate analyses of specimen length and width, that demonstrate gross shape disparity: 1) *P. minchami*, specimens of which are laterally wider, whilst 2) *P. saggita* specimens are comparatively narrower. To more comprehensively assess the shape variability in the genus, I apply geometric morphometric shape analyses to 213 specimens from Ediacara Conservation Park, Nilpena and the White Sea of Russia collectively, revealing a continuous gradient in shape change from wide specimens through to narrow specimens. In light of the variability observed in its shape, I argue that the two currently described taxa are possibly extreme morphotypes of a species that demonstrates a high degree of morphological plasticity.

In this thesis I also describe a new Ediacaran fossil with bilateral symmetry from Ediacara Conservation Park, an organism I have named *Velocephalina greenwoodensis*. This fossil shows a body structure previously undescribed among the Ediacaran genera, although it does share some similarities with the mollusc-grade Ediacaran fossil *Kimberella*. As such, I interpret *Velocephalina* to be a possible stem-group mollusc, and also suggest that bilaterian organisms were likely more prolific during the Ediacaran period than previously thought.

Finally, I examine the palaeoecology of major fossil beds excavated from Nilpena using species-diversity models applied to living communities, to see if the same ecological assembly rules pertained to the earliest complex communities on Earth. The species-area richness (SAR) model, $S = cA^z$, where species richness (*S*) increases as a power function (*z*) of habitat area (*A*), is a fundamental ecological law that applies to all living communities. I apply the fundamental ecological law of SAR to a sample of 18 Ediacaran seafloor surfaces from Nilpena to see if the same ecological assembly rules pertained to some of the earliest communities on Earth. Remarkably, despite a lack of predation –one of the main drivers of Phanerozoic evolution– in the sampled Ediacaran communities, and vast changes in species composition, this study demonstrates that this fundamental ecological assembly rule persisted for over half a billion years.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

I acknowledge that copyright of published works contained within this thesis resides with the copyright holder(s) of those works. I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time. I acknowledge the support I have received for my research through the provision of an Australian Government Research Training Program Scholarship.

Felicity J Coutts

Signed … ……

Date ...30 January 2019........

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Chapter 1: Introduction

1.1 Contextual Statement

My thesis contributes to the collective knowledge of early multicellular life on Earth by presenting analyses of select Ediacaran organisms and communities preserved in late Precambrian fossilised seafloors. Although the evolutionary importance of the Ediacaran biota has been studied for more than 100 years, thanks to modern analytical techniques we are still learning much about these ancient communities.

In Chapter 2 and the first publication of this thesis I begin by broadly examining the palaeoecology of a specific fossil bed excavated from northern Ediacara Conservation Park — coded 'NECP Bed-1' — remarking specifically on the prevalence of juvenile forms of the shield-shaped Ediacaran fossil *Parvancorina*. This is the first time in over 50 years that fossils from this particular fossil site have been examined in detail and on such a large scale. NECP Bed-1 preserves the smallest examples of *Parvancorina* found anywhere in the world, likely attributable to the fine grain size preserving the fossils from this locality. Furthermore, this bed hosts a highly diverse Ediacaran community. The presence of juvenile specimens allows for the evaluation of morphological development, and also raises questions about how the role of sand grain size effects fossil resolution. In the first chapter I therefore open up the potential for analyses and discussion into the morphological development and preservational influences of *Parvancorina* and other fossils.

In Chapter 3 (second publication) I continue to explore aspects of the *Parvancorina* population on NECP Bed-1 from ecological and morphological perspectives, about which we currently know little. I applied spatial analyses to assess specimen spatial densities and found a divergence in the morphology between juvenile and adult specimens, such that the anchor-shaped ridge, characteristic of *Parvancorina*, was more pronounced in smaller specimens. For the first time among any Ediacaran fossil, a strong bimodal orientation was revealed among the juvenile specimens on this bed, and might bear relevance to *Parvancorina* behaviour and interactions with benthic currents.

In Chapter 4 (submitted manuscript), *Parvancorina* is explored from a morphological perspective using *Geomorph*, a landmark-based geometric morphometric analysis program. For the first time, I examined the shape of this fossil in quantitative detail. Little is known about the phylogenetic affinities of *Parvancorina*, let alone most Ediacaran forms, although two species of *Parvancorina* have been described using the regression of length and width alone. In this chapter I present new findings on *Parvancorina* ontogeny, where its dorsal morphology of the fossil changes with growth. Further, I reveal evidence to refute the differences between the two currently described species, and to consider them as a single species instead.

In Chapter 5 (unpublished manuscript), I describe a recently discovered Ediacaran fossil with bilaterial symmetry from Ediacara Conservation Park, also mentioned in the first paper of this thesis, and assign it a new genus and species. This fossil, *Velocephalina greenwoodensis*, presents unique characters relative to all other Ediacaran forms found to date; however, it is somewhat similar to the Ediacaran fossil organism *Kimberella*, described as one of the earliest stem-group molluscs. Importantly, the discovery of this new fossil, not long after observing large expanses of fine-grained, fossilised Ediacaran seafloor from Ediacara Conservation Park, suggests that further excavation and observation of these surfaces could reveal additional new species.

Finally, in Chapter 6 (unpublished manuscript) I convey a sense of symmetry with the first paper by focussing on Ediacaran seafloor palaeoecology at the end of the thesis. In this chapter, a fundamental ecological assembly rule that governs all living communities today, the species-area relationship, was applied to samples of Ediacaran communities from Nilpena to see if these ancient communities were also governed by the same ecological laws. This is the first time the species-area relationship has been applied to ancient Ediacaran seafloors. Like the genes that transcribe the blueprint of life, perhaps these ecological assembly rules are also inherent throughout biological time.

1.2 Background and review of relevant literature

The Ediacaran Period (ca. 635 to 541 Ma; Martin *et al*. 2000; Knoll *et al*. 2004; Linneman *et al*. 2018) marks the first appearance of large, complex multicellular life on Earth — the Ediacara biota. The Ediacara biota are a diverse array of benthic marine organisms preserved as impressions and carbonaceous compressions in siliciclastic deposits (Gehling 1991; Narbonne 2005; Pu *et al*. 2016; Droser *et al*. 2017). Since the discovery and identification of the first Ediacaran body fossil over 100 years ago in Newfoundland, Canada (Billings 1872), hundreds more have been discovered in over 40 countries world-wide (Sprigg 1947; Germs 1972; Ivantsov 1999; Gehling & Narbonne 2007; Feng *et al*. 2008; Narbonne *et al*. 2009).

Three major Ediacaran fossil assemblages have been established, which summarise three distinct taxonomic compositions, preservation styles, and generalized submarine environments in which Ediacaran communities thrived (Waggoner 2003; Narbonne 2005; Boag *et al.* 2016; Droser *et al*. 2017). Fossils of the oldest Ediacaran fossil assemblage, the ‘Avalon Assemblage’, are found in Newfoundland, eastern Canada, and Charnwood Forest, England (579–560 Ma; Ford 1958; Benus 1988; Bowring *et al*. 2003; Pu *et al.* 2016). These fossils are defined by their large and structurally complex ‘frondose’ or ‘plume’-shaped architecture and deep-water settings (Misra 1969; Wood *et al*. 2003). Next, Ediacaran fossils of the ‘White Sea Assemblage’ (~ 555 Ma; Martin *et al*. 2000), found in the White Sea of Russia and the Flinders Ranges of South Australia, show morphological advances and arguably the advent of the first metazoans (Martin *et al*. 2000; Seilacher *et al*. 2003; Waggoner 2003; Grazhdankin 2004). Finally, nearing the end of the Ediacaran period and terminal Proterozoic Era, the ‘Nama Assemblage’ is dated between 549–541 Ma (Grotzinger *et al*. 1995; Linneman *et al.* 2018). Fossils of the Nama Association consist of mainly frondose forms with complex compartmentalisations, as well as early calcified metazoans and bilaterian burrows (Narbonne 2005). The Nama Association also exhibits the unique transition from ‘soft-bodied’ Ediacaran biota to the sclerotised and mineralised metazoans of the Cambrian Period (Gehling 2007).

1.2.1 Ediacaran fossils of the Flinders Ranges, South Australia

Ediacaran fossils of the Flinders Ranges in South Australia are diverse, and uniquely incorporate organisms found in all three Ediacaran fossil assemblages. Whether or not these enigmatic organisms represent the first appearance of metazoans has been the focus of much debate since the discovery of the first Ediacaran form found in the Flinders Ranges of South Australia by Sprigg in 1947 (Sprigg 1947). Fossils are preserved as shallow external moulds in the soles of stratified siliciclastic sedimentary rock that was once the late Precambrian sea floor. They are considered to have been largely benthic, soft-bodied organisms (Glaessner 1984; Gehling 1991; Narbonne 1998); however, the consistently resistant preservation of some forms suggests a degree of body sclerotization (Clites *et al*. 2012; Penny *et al*. 2014). Additionally, recent morphological observations of a new, possibly pelagic Ediacaran fossil from Nilpena, *Attenborites janeae* (Droser *et al*. 2018), suggest that pelagic organisms might have existed, however escaped preservation. Several Ediacaran forms seem to display synapomorphies (shared characters) with living phyla such as Mollusca, Cnidaria, Ctenophora, Porifera and Arthropoda (Conway Morris 1990; Fedonkin & Waggoner 1997; Zhu *et al*. 2008; Clites *et al*. 2012). Subsequently, some have argued that several Ediacaran organisms persisted into the Cambrian Period (541–485 Ma; Knoll & Carroll 1999; Jensen *et al*. 1998; Zhang *et al*. 2003; Lin *et al*. 2006), famous for the appearance and diversification of most major animal lineages (Zhuravlev & Riding 2000).

Despite abundant evidence of movement, feeding strategies, and basic morphological characteristics that most animals share (i.e., bilateral symmetry, antero-posterior and dorso-ventral asymmetry), the animal affinities of some Ediacaran organisms have been debated (Retallack 2013). Just a few interpretations of the Ediacara biota include an extinct clade of life altogether known as the Vendobionta (Buss & Seilacher 1994), protists (Zhuravlev 1993), lichens (Retallack 1994), microbial colonies (Steiner & Reitner 2001), and fungal-grade organisms (Peterson *et al*. 2003). However, Bobroskiy *et al*. (2018) recently discovered lipid biomarkers, regarded as unique to animals, in specimens of the Ediacaran fossil *Dickinsonia* from the White Sea in Russia. This finding is remarkable, particularly because Ediacaran fossils were previously thought to be depauperate of organic material. Importantly, this finding also suggests that other Ediacaran organisms morphologically similar to *Dickinsonia* might also have had a metazoan affinity.

Ediacara Conservation Park and the National Heritage-listed fossil site Nilpena are the most prominently researched Ediacaran fossil sites in the Flinders Ranges (see Fig. 1). The ~ 35 km stretch of Ediacaran and Cambrian strata exposed at Ediacara Conservation Park and Nilpena form a faulted succession, separated from the main ranges by a syncline. The first Australian Ediacaran fossil was discovered in Ediacara Conservation Park in 1946 (Sprigg 1947, Glaessner 1958), and subsequently, Ediacaran fossils have been discovered

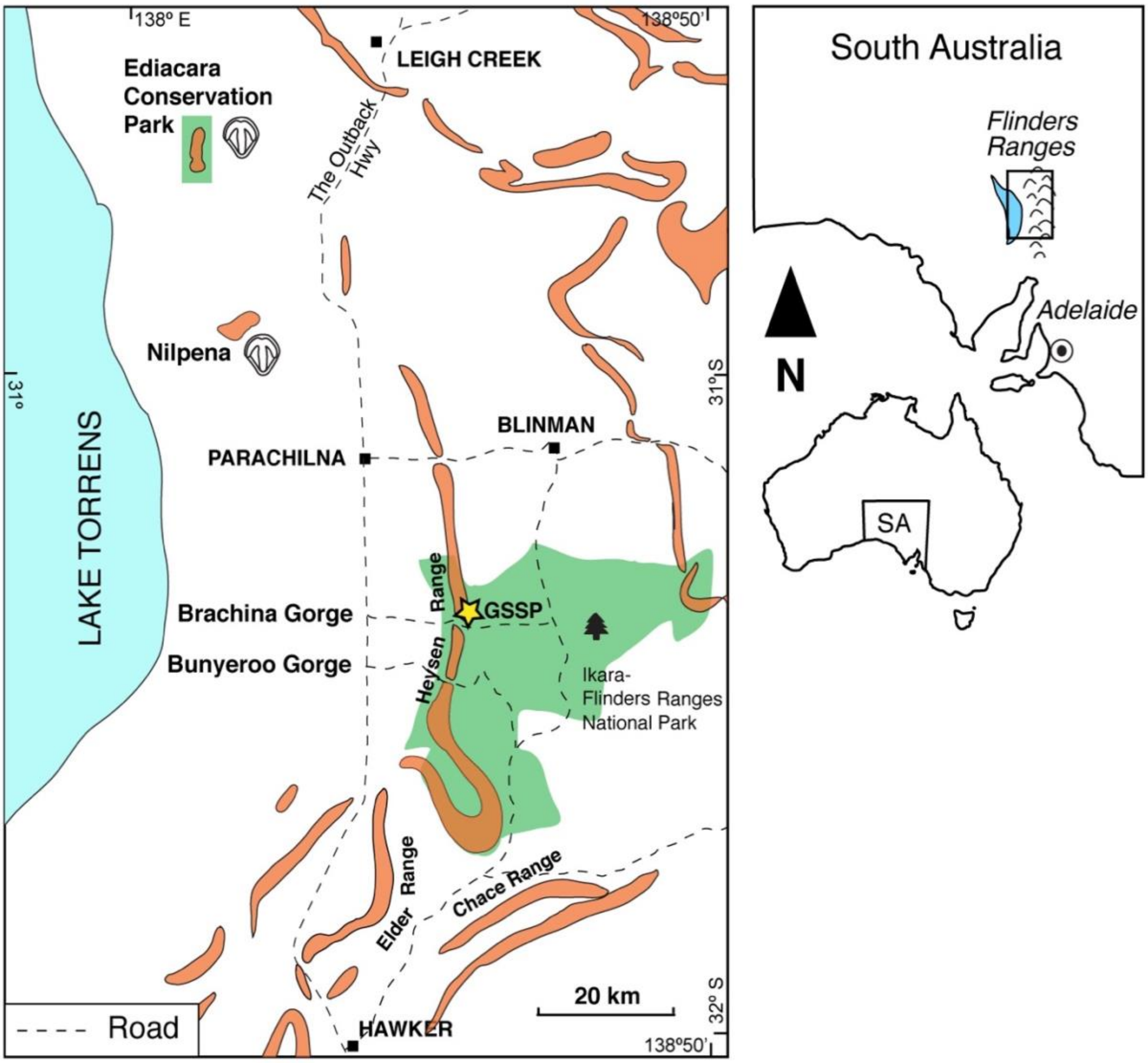

Figure 1. Map showing location of the main Ediacaran fossil sites studied in this thesis: Ediacara Conservation Park and Nilpena in the western Flinders Ranges. Orange-shaded regions indicate fossiliferous Ediacaran outcrop. The Ediacaran Period Global Stratotype Section and Point (GSSP) is marked with a yellow star. Figure adapted from Gehling & Droser (2012).

throughout the Flinders Ranges region (orange shaded areas in Fig. 1; Gehling 2000). In 2006, the International Union of Geological Sciences approved the Ediacaran period as a new period of time, and a ‘Golden Spike’, marking the Global Stratotype, Section and Point (GSSP) of the Ediacaran Period was erected in the Ikara-Flinders Ranges National Park near Brachina Gorge (star icon in Fig. 1).

Ediacara Conservation Park and Nilpena make excellent field laboratories in which to study Ediacaran seafloor communities, because both sites are highly fossiliferous, demonstrate high taxonomic diversity, and large expanses of fossilised seafloors can be excavated and laid out for observation (Gehling & Droser 2013; Droser *et al*. 2017).

Over 30 different species have been identified from the Ediacara Member of the Flinders Ranges, and dozens more unidentified forms have yet to gain official descriptions.

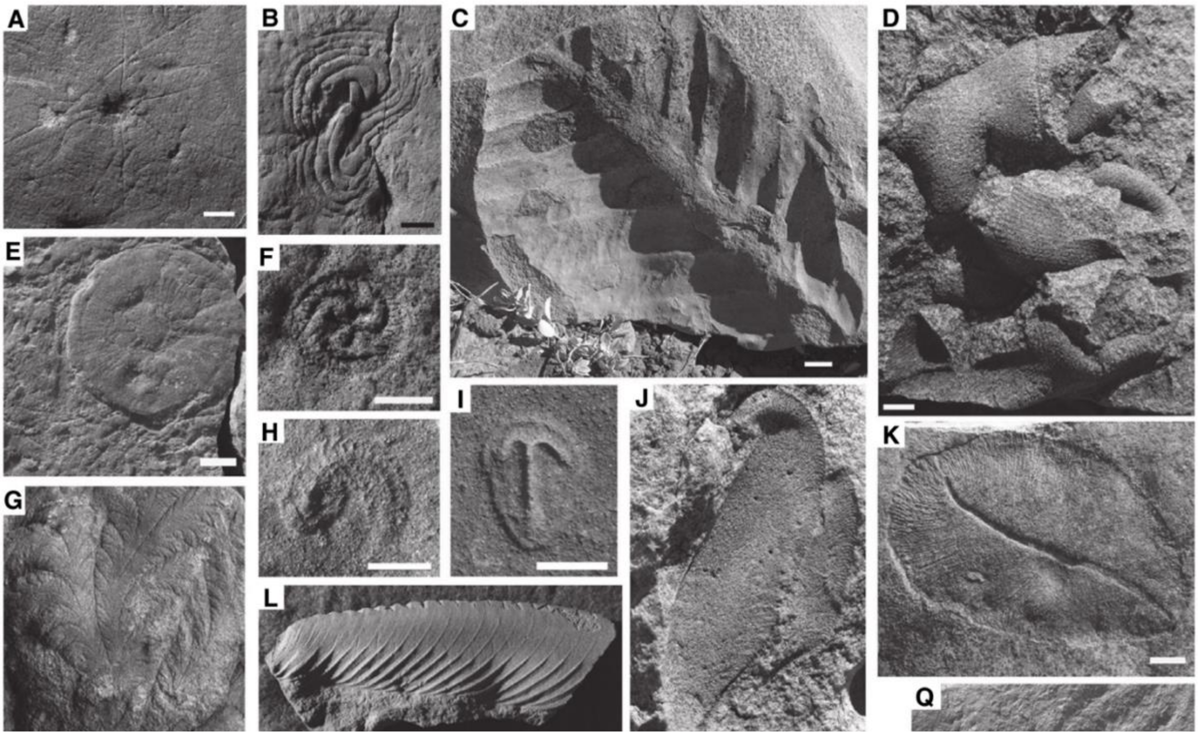

Figure 2. Examples of Ediacaran fossils found in the Ediacara Member of the Rawnsley Quartzite of the Flinders Ranges, South Australia. **A.** *Coronacollina acula.* **B.** *Eoandromeda octobrachiata*. **C.** *Charniodiscus* sp. **D.** Ripped and contorted *Dickinsonia* sp. **E.** *Aspidella terranovica* and *Funisia dorothea*. **F.** *Tribrachidium heraldicum* **G.** Rangeomorph. **H.** *Spriggina floundersi*. **I.** *Parvancorina* sp. **J.** *Nasepia* sp. **K.** *Dickinsonia tenuis.* **L.** *Pteridinium* sp. **M.** *Archaeichnium* sp. **N.** *Archaeichnium*. **O.** *Dickinsonia costata.* **P.** *Helminthoidichnites*. **Q.** *Charnia* sp. Figure modified from Gehling & Droser (2013).

In Chapter 5 of this thesis, a new Ediacaran genus and species, *Velocephalina greenwoodensis*, is described from Ediacara Conservation Park. A few examples of iconic Ediacaran fossils found in Ediacara Conservation Park and Nilpena include: *Coronacollina* (Fig. 2A), *Eoandromeda* (Fig. 2B), *Charniodiscus* (Fig. 2C), *Dickinsonia* (Fig. 2D, K and O), *Aspidella* (Fig. 2E), *Tribrachidium* (Fig. 2F), *Spriggina* (Fig. 2H) and *Parvancorina* (Fig. 2I).

The observation and analysis of fossil surfaces from Ediacara Conservation Park reveal that many small organisms frequented the Ediacaran sea floor, some no larger than 2 mm in length (Coutts *et al*. 2016). Most specimens are identifiable as small *Parvancorina* (Fig. 2I; Glaessner 1958), and some are unknown and are as yet unreported (Waggoner 2003). The biological affinities of the characteristically shield-shaped organism *Parvancorina* are largely unknown, and characteristics such as reproduction mode, feeding mode, or even number of species of the taxon is understudied and as such requires further investigation.

The Ediacaran fossil *Parvancorina*

The Ediacaran fossil genus *Parvancorina* is not well known, and few papers have been published on this enigmatic organism. *Parvancorina* was first described by Glaessner (1958) through observations of several specimens from the Rawnsley Quartzite in the Flinders Ranges. Glaessners' last thorough analysis of *Parvancorina* involved further observations of 60 specimens, where he collected data on morphology and measured individual length and width (Glaessner 1980). He first coined descriptive terms for *Parvancorina* morphology such as: medial ridge (a narrow ridge centrally spanning the organism from one end of the body to the other), and anterolateral ridges (lateral ridges that connect to the medial ridge, and

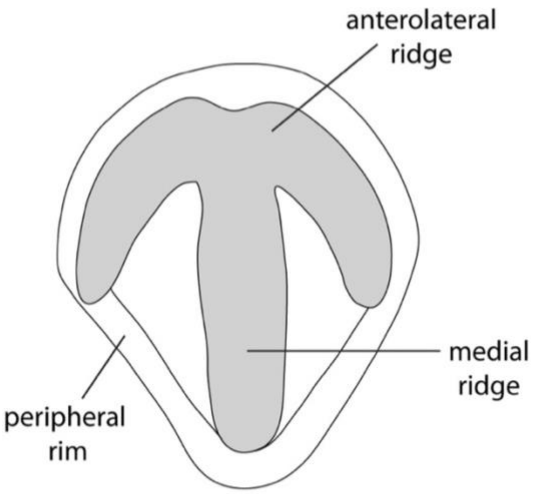

Figure 3. Simplified illustration of *Parvancorina* specimen.

together comprise an anchor-shape). In this thesis, I will refer to the anterolateral ridges as a single *anterolateral ridge*, which laterally spans the organism (Fig. 3). Glaessner (1980) suggested the presence of several size classes within the genus, although no official analyses were done. Since 1980, a few other papers have discussed the phylogenetic affinities of *Parvancorina.* Zhang *et al*. (2003) reconsidered the previous interpretation of a fossil Naraoiid from the lower Cambrian of South China as a Parvancorinomorph, notably *Primicaris larvaformis*. These authors also pointed out that the morphological similarity between the Ediacaran genus *Parvancorina* and the Cambrian organism *P. larvaformis* might be indicative of an evolutionary link between the two geological periods of time. Later, Lin *et al*. (2006) revealed the discovery of a lower-middle Cambrian arthropod (*Skania sundbergi*) with striking dorsal morphology analogous to *Parvancorina*. Both publications suggested possible arthropod affinities for *Parvancorina*. Molecular dating studies have demonstrated that arthropod evolution and diversification predated the Cambrian, occurring during the Ediacaran (Rehm *et al*. 2011; Rota-Stabelli *et al*. 2013). However, other palaeontological analyses suggest that *Parvancorina* lacks compelling characters shared with Arthropoda (Edgecombe & Legg 2014). Therefore, the phylogenetic affinities of *Parvancorina* are still debated.

So far, only one species (*Parvancorina minchami* Glaessner 1958) has been described from the Flinders Ranges of South Australia, and two species, *P. minchami* and *P. sagitta* have been described from the White Sea of Russia (Ivantsov *et al*. 2004). These authors used bivariate regression of the length and width of specimens to test whether there was evidence of more than one morpho-type in the genus. The results suggested the presence of two different species, *P. minchami* and *P. sagitta*; however, they used a small sample group (*n* = 35) and did not statistically test the relationship. Later, Naimark & Ivantsov (2009) did a large morphometric analysis of *Parvancorina* from the White Sea, and included a small subset of specimens from the Flinders Ranges of South Australia. Their study also recognised the presence of two species, although it was also restricted to using the parameters of length and width alone. A thorough multivariate analysis of *Parvancorina* body plans from the Flinders Ranges has not been conducted as yet, therefore the analytical methods I applied in Chapters 2–4 of this thesis will help to elucidate any morphological patterns seen within the genus *Parvancorina*, and hence any morphological variants.

Preservation

Approximately 555 million years ago, communities of Ediacaran organisms lived in shallow marine, deltaic environments in a submarine basin that is now the tectonically uplifted and eroded Flinders Ranges (Gehling & Droser 2012). Textured organic surfaces (Gehling & Droser 2009) are present on all fossiliferous surfaces and suggest that the Ediacaran seafloor was covered in an organic film or mat, possibly of bacterial or algal origin (Jenkins *et al*. 1983; Gehling 1999; Seilacher *et al*. 2005; Droser *et al*. 2006). These largely uninterrupted biological films proliferated due to the lack of vertically burrowing organisms, which would have extensively bioturbated the substratum. The biological innovation of bioturbation does not appear in the fossil record until the beginning of the Cambrian Period

(Vannier *et al*. 2010). Benthic organisms interacted with this organic mat, with some relying on it for food. The Ediacaran stem-group mollusc *Kimberella* actively grazed the surfaces of this mat, leaving paired sets of fanned grooves in the seafloor (Ivantsov & Fedonkin 2001; Seilacher *et al*. 2005). The organism *Dickinsonia* also left depressions on the mat surface where it was presumably stationary for periods of time, dissolving and consuming the organic mat beneath it (Gehling *et al*. 2005). Importantly, with the exception of the rice-grain sized bilaterian that displaced sand to create groove and levee trace fossils (see *Helminthoidichnites* in Fig. 2P; Gehling & Droser 2018), trace fossils as a result of mobility alone are rarely preserved in the Ediacaran seafloor of the Flinders Ranges.

The mode by which Ediacaran fossil surfaces were preserved is a compelling concept, and has been the subject of recent debate. Through observations of Ediacaran fossils of the Flinders Ranges, Gehling (1999) originally proposed the “death mask” model of preservation (Fig. 4), whereby, textured organic surfaces prevalent across Ediacaran

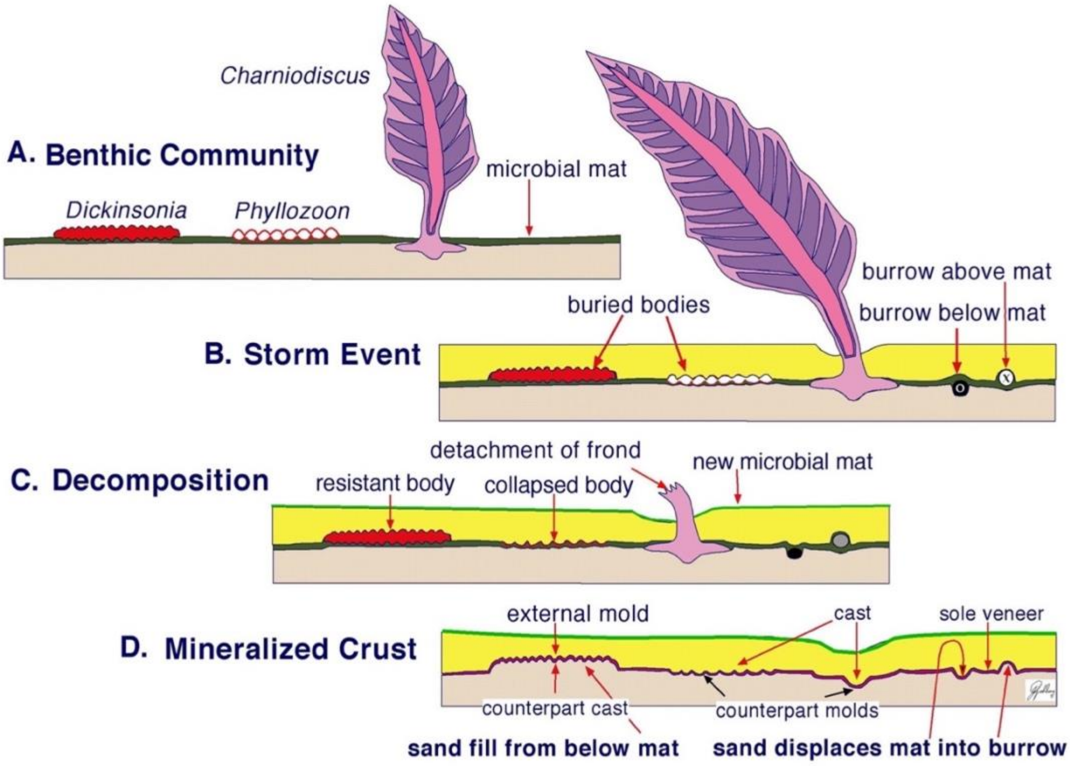

Figure 4. Illustration of an Ediacaran bed explaining the "death mask" model of preservation for common Ediacaran taxa *Dickinsonia*, *Phyllozoon*, *Charniodiscus* and the burrowing organism *Helminthoidichnites*. **A.** Shows the benthic community as it was in life, with the organisms living on and within the microbial mat. **B.** Storm-mediated events stir up sand and rework sediment before depositing it on the benthic community. Organisms that sit erect in the water column (i.e. *Charniodiscus*) can be torn from their holdfasts. **C.** Organisms decompose beneath the top layer of sand. **D.** Hydrogen sulphide from bacterial decay and reduction of sulphate reacted with iron oxides in the sediment (Berner, 1969, 1970) to precipitate a 'sole veneer' of iron sulphide encrusting the contours of the seafloor and constituent organisms (Gehling 1999). Figure from Gehling (1999).

seafloors played an important role in the exquisite preservation of Ediacaran fossils by enabling the precipitation of an iron-pyrite coating over the communities. This model of preservation was later corroborated in fossil surfaces from the Avalon assemblage of Newfoundland, Canada (Laflamme *et al*. 2011; Darroch *et al*. 2013; Liu 2016). After, Tarhan *et al*. (2016) proposed an alternative 'early silicification model' for Ediacaran fossil preservation globally. This model proposes that the rapid precipitation of silica cements in the early stages of Ediacaran seafloor diagenesis facilitated sand grains to mould the contours of the organic mats and organisms (Tarhan *et al*. 2016). A more recent analysis by Liu *et al*. (2019) of Flinders Ranges material disputes this, however, and instead favours the original death mask model (Liu *et al*. 2019). Please see Figure 4 above for a more detailed explanation of the death mask model as it applies to Flinders Ranges Ediacaran fossils.

Sedimentation events caused the repeated burial of Ediacaran communities in sand flows (Gehling 1999; Fedonkin *et al*. 2007), casting the dorsal external forms of the organisms and lithifying, preserving a death mask of the ancient communities on the soles of the beds above the seafloor (see Fig. 4; Gehling 1999). Consequently, these communities appear as largely concaved impressions in the bed above what was once the seafloor. This unique mode of preservation has resulted in vast expanses of fossilised Ediacaran seafloor

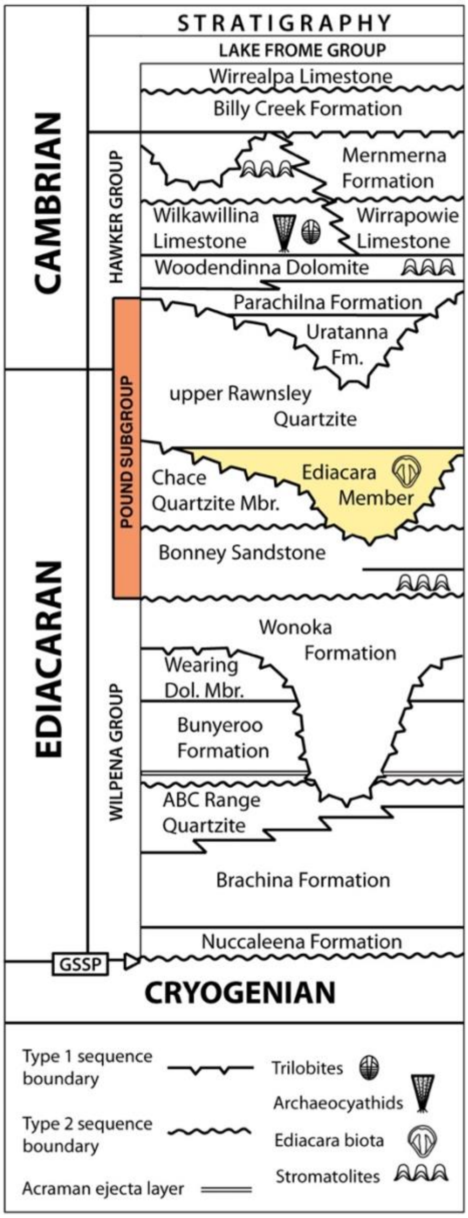

Figure 5. Stratigraphic chart of Precambrian and Cambrian sediments showing the relative position of the fossiliferous Ediacara Member within the Pound Subgroup and lower Rawnsley Quartzite. Figure modified from Gehling &

communities preserved *in situ*, as they were in life at the time of burial (Gehling 1999).

Many quartz sandstone horizons preserving Ediacaran fossils are found within the fossiliferous Ediacara Member in the upper Rawnsley Quartzite of the Pound Subgroup (Fig. 5). Within the Rawnsley Quartzite, fossiliferous Ediacara Member strata fill a submarine basin that ranges from 5- to 150-m thick at the basin margins, and it incises valleys 300 m deep into the strata of the Chace Quartzite Member and Bonney Sandstone below (Fig. 5; Gehling 2000; Gehling & Droser 2009). The upper part of the Ediacara Member contains five different facies of fossiliferous beds with each succession under 10 m thick, sand grains vary between diameters of 0.1 and 0.5 mm, and the resolution of preserved detail improves with a decrease in grain size (Droser & Gehling 2008). These facies demonstrate varying submarine environments, ranging between shallower- through to deeper-water settings, and include: 1) shore-face sands, 2) oscillation-rippled wave-base sands, 3) flat-laminated to lingoid rippled delta-front sands, 4) planar-laminated sheet-flow sands and 5) channelised mass-flow sands (Gehling & Droser 2013; Tarhan *et al*. 2017). As one might expect, the taxonomic composition of Ediacaran communities relied on the immediate submarine environment, and therefore specific taxa are restricted to certain facies (Gehling & Droser 2009; Tarhan *et al*. 2014; Reid *et al*. 2018).

Palaeoecological analyses

Unlike today's biologists who have access to the soft-tissue and DNA of living organisms, Ediacaran palaeontologists must use largely phenotypic and taphonomic clues to draw comparisons between the morphology of different organisms. Ediacaran fossils contribute to the evolution of early complex, multicellular life on this planet, and controversial perspectives can be popular. It is therefore imperative that robust analytical methods are explored and applied to these fossil communities to ensure repeatable results.

Some Ediacaran forms from South Australia display morphological organisation found exclusively in metazoans, namely bilateral symmetry, antero-posterior differentiation, allometric growth patterns (Lin *et al*. 2006), self-powered locomotion (Gehling *et al*. 2005; Ivantsov 2009), and evidence of grazing (Fedonkin & Waggoner 1997; Seilacher *et al*. 2005; Gehling *et al*. 2014). However, other ecologically salient characteristics such as reproduction, competition, and predation are more difficult to assess due to the limited, almost two-dimensional nature of Ediacaran preservation. To address this limitation, computer-based spatial and morphometric analyses are increasingly used to elucidate ecologically relevant phenomena, such as growth and development (Laflamme & Casey 2011), competition (Clapham *et al*. 2003), reproduction (Darroch *et al*. 2013; Mitchell *et al*. 2015), and dispersal (Droser & Gehling 2008; Mitchell *et al*. 2015).

Traditional morphological analyses consist of size comparisons using the parameters of length and width of simple homologous characters among a series of specimens. From these data, simple regression plots comparing the length:width ratio of a series of specimens can be produced, and show how these measurements vary among individuals. While these more traditional morphometric analyses are informative, they are limited to measuring the parameters of length and width alone. On the other hand, modern morphometric methods such as geometric morphometrics are more informative and enable the user to analyse the complex shape change of characters across individuals (Dryden & Mardia 1998; Klingenberg 2011; Laflamme *et al*. 2004; Laflamme *et al*. 2007; Laflamme & Casey 2011).

Geometric morphometrics uses homologous, anatomically consistent landmarks (points) across a series of specimens, and measures the amount of displacement between these landmarks (Laflamme & Casey 2011), revealing morphological differences among specimens. This is primarily achieved by the removal of the influences of size, rotation and translation (Zelditch *et al.* 2004) through superposition methods (Rohlf & Slice 1990). At this stage, few geometric morphometric analyses have been applied to Ediacaran taxa (Laflamme & Casey 2011; Paterson *et al*. 2017); however, these have provided important morphological information about the fossils at hand. For instance, Laflamme & Casey (2011) used geometric morphometrics to analyse the shape and modular variation within a single species of *Charnia* (Fig. 2C). They used only four landmarks (due to uncertainties of other anatomically consistent points), from which they found lateral variation in the segments among different specimens. Compared to traditional approaches, geometric morphometrics allowed them to test for more complex morphological differences, and provided more confident inferences about the structure of the organism. In Chapter 4 of this thesis, I apply such geometric morphometric methods to a large population of *Parvancorina* to eludicate any apparent trends in morphology and shape.

The amount of ecological information that can be extracted from studies of fossil communities is often limited, i.e., Phanerozoic fossil communities are often preserved as time-averaged death assemblages (where pelagic and benthic organisms are fossilised inside a sedimentary matrix) and their original spatial conformations are lost (Kidwell 2001). On the contrary, the Ediacara Member of the Flinders Ranges preserves entire Ediacaran communities *in situ* (in place), basically as they were in life, but possibly with the presence of recently dead and decaying individuals. It is because of this unique type of preservation, and lack of bioturbation of Ediacaran seafloors, that make these communities ideal examples on which to study the ecology of some of Earth's earliest complex life.

Spatial analyses including cluster analysis and nearest-neighbour methods are used to investigate associations among living taxa (Wiens 1989; Wälder and Wälder 2008), and thus can also be applied to Ediacaran communities to reveal how organisms interacted within ancient communities (Darroch *et al*. 2013; Mitchell *et al*. 2015). For instance, Mitchell *et al*. (2015) used nearest-neighbour cluster analyses to investigate the spatial distribution patterns in a population of the iconic fusiform-shaped fossil *Fractofusus* (a type of Rangeomorph, see Fig. 2). Remarkably, through their analysis Mitchell *et al*. (2015) argued for a possible stolon-like reproductive mode for *Fractofusus*. Understanding the ecological affinities, interactions or associations of Ediacaran organisms requires the additional interpretation of spatial distributions because they are inextricably and causally linked (Tilman 1994). Furthermore, space is a resource, and species-diversity and spatial patterns are linked to this occupation of space (Heip 1975; Jackson 1977). Therefore, ecological assembly rules that govern modern communities should also be theoretically applicable to Ediacaran fossil communities. For instance, the species-area relationship (SAR), $S = cA^z$, where species (S) accumulate as a power-law function (z) over areas of landscape (A), is a fundamental ecological tool used for assessing the conservation risk of species within habitats (Giam *et al*. 2011). The static, *in situ* preservation of Ediacaran communities and lack of pre- and post-burial sediment bioturbation provide ideal examples on which to apply ecological assembly models such as this. Chapter 6 of this thesis explores the species-area relationship as it is applied to Ediacaran seafloors from Nilpena; the repercussions of which could provide insights into community ecology spanning half a billion years.

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Chapter 2

How diverse were early animal communities?

An example from Ediacara Conservation Park, Flinders Ranges, South Australia

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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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How diverse were early animal communities? An example from Ediacara Conservation Park, Flinders Ranges, South Australia

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Fossils of the Ediacara biota record the earliest evidence of animal communities and, as such, provide an invaluable glimpse into the abiotic and biotic processes that helped shape the evolution of complex life on Earth. A diverse community of Ediacaran macro-organisms is preserved with high resolution in a fossil bed recently excavated from north Ediacara Conservation Park (NECP) in the Flinders Ranges, South Australia. Many of the commonly described Ediacaran taxa from the Flinders Ranges are represented on the bed surface and include: *Parvancorina*, *Rugoconites*, *Spriggina*, *Dickinsonia*, *Tribrachidium*, *Kimberella*, *Charniodiscus* and *Yorgia*, including two new taxa. Numerous additional fossil-bed fragments from the same locality were analysed that preserve a similar suite of taxa and shared sedimentology. On all surfaces, preserved microbial mat appeared complex, both in topography and in texture, and the unique combination of fine grainsize, high diversity and trace fossils provide insights into the palaeoecology of the ancient organisms that lived during the Ediacaran Period some 550 Ma. Several trace fossils are overlapped by body fossils, indicative of successive events, and complex organismal behaviour. The complexity of this fossil surface suggests that the primordial community was relatively mature and possibly at late-stage succession.

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THE EDIACARAN Period (635–542 Ma; Knoll *et al.* 2006) records the earliest evidence of complex animal life on Earth (Glaessner 1959a, Gehling 1991, Fedonkin & Waggoner 1997), and the Ediacara biota of South Australia incorporates the most morphologically and taxonomically diverse assemblages yet discovered within this interval (Droser *et al.* 2006, Bambach *et al.* 2007, Shen *et al.* 2008, Droser & Gehling 2015). Collectively, the fossil organisms have morphological organizations characteristic of animals, namely: bilateral symmetry (Fedonkin & Waggoner 1997), anteroposterior asymmetry (Bambach *et al.* 2007), allometric growth patterns (Lin *et al.* 2006), evidence of locomotion (Gehling *et al.* 2005, Ivantsov 2009) and evidence of grazing (Fedonkin & Waggoner 1997, Seilacher *et al.* 2005, Gehling *et al.* 2014). However, assessments of ecologically influential factors, such as reproduction, sexual dimorphism, predation and competition are less straightforward in the Ediacaran fossil record.

Past studies have focused primarily on the taxonomic interpretations of the Ediacara biota. Almost every Ediacaran genus has been described as the ancestor of phyla that exist today, and much research effort has been placed on the reinterpretation of previously described taxa (Glaessner 1959b, Glaessner 1966, Glaessner & Wade 1966, Manton & Harding 1967, Fedonkin & Waggoner 1997, Gold *et al.* 2015). For instance, Glaessner & Daily (1959) initially described *Kimberella* as a jellyfish before it was shown to be associated with grazing traces and subsequently described as a mollusc-like bilaterian (Fedonkin & Waggoner 1997, Ivantsov 2013, Gehling *et al.* 2014). These taxonomic analyses are relevant and necessary. However, there is a limit to the amount of biological information that can be obtained from these interpretations owing to taphonomic constraints, grainsize and the area of fossil bed able to be studied. The average grainsize of a bed determines the resolution observed on a fossil surface, and the surface area of an intact fossil bed, determines the degree to which the palaeoecology of a community can be analysed. Thus, the study of large bedding surfaces bearing fossils can provide insights into the palaeoecology of the Ediacara biota and the constituent organisms' autecological and synecological interactions (Clapham & Narbonne 2002,

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Clapham *et al.* 2003, Droser *et al.* 2006, Mitchell *et al.* 2015).

Adding to the controversy surrounding the affinities of the Ediacara biota, an outlying perspective argues that Ediacaran macro-organisms consisted of terrestrial lichens and fungi (Retallack 2013), disregarding the abundant evidence of submarine sedimentation (Gehling 2000, Gehling & Droser 2012, Tarhan *et al.* 2015) and morphological traits shared with animals (Gehling *et al.* 2005, Bambach *et al.* 2007, Ivantsov 2009). Furthermore, taphonomic analysis shows that many Ediacaran organisms had soft and thin bodies, which would desiccate quickly in terrestrial environments (Glaessner 1959a, Gehling 1991, Narbonne 1998, Ivanstov *et al.* 2014). For this reason, it is important to observe not just single specimens, but also community samples so that fundamental synecologies are considered.

Over the last 15 years, increasing numbers of studies have focused on the interpretation of *in situ* Ediacaran communities, with the aim of elucidating specific ecologically influential characteristics, such as reproduction mode and competition. Several studies have investigated the structure of temporally older Ediacaran communities on the exposed coastal outcrops of SE Newfoundland in Canada (Clapham & Narbonne 2002, Clapham *et al.* 2003, Darroch *et al.* 2013). Studies of Flinders Ranges fossils (South Australia) have examined the autecology of single genera on beds (Droser & Gehling 2008, Evans *et al.* 2015, Hall *et al.* 2015). However, few Australian studies have considered multiple taxa on the same bed (Droser *et al.* 2006). Gradually, as more complete fossil surfaces are excavated and assembled, it is anticipated that the palaeoecology of the Ediacara biota will become better understood (Clapham & Narbonne 2002, Clapham *et al.* 2003, Droser *et al.* 2006, Darroch *et al.* 2013).

Geological setting

Although Ediacaran fossils are known from over 40 localities around the world (Xiao & Laflamme 2008), three main fossil associations have been identified (Waggoner 2003). These comprise different taxonomic assemblages, demonstrate varying taphonomic and environmental conditions, and possibly occupied separate periods in time spanning 575–542 Ma (Gehling 1999, Fedonkin 2003, Grazhdankin 2004, Gehling & Droser 2013). Radiometric dating has identified the oldest Ediacaran fossils in the Avalon association (Newfoundland and England) between 575–560 Ma; fossils from the White Sea association (Russia and eastern Europe, Siberia and South Australia) in the late Ediacaran, at around 555 Ma; and the Nama association (Namibia and Western USA) contains the youngest fossils in the terminal Ediacaran between 549 and 542 Ma (Narbonne 2005).

The White Sea association of South Australia has the greatest generic and morphological diversity of any known Ediacaran assemblage (Droser *et al.* 2006, Bambach *et al.* 2007, Shen *et al.* 2008); including elements of the Avalon and Nama associations (Gehling & Droser 2013, Meyer *et al.* 2014, Droser & Gehling 2015). Approximately 550 million years ago, communities of Ediacaran organisms lived in shallow, marine deltaic environments in a submarine basin between the fair-weather and storm wave-bases (Gehling 2000, Droser *et al.* 2006, Gehling & Droser 2013). Ediacaran fossils are preserved in the Ediacara Member of the Rawnsley Quartzite, within the Pound Subgroup (Sprigg 1947; Fig. 1B), exposed at numerous locations within the Flinders Ranges (Fig. 1A). The fossil-bearing sandstone facies of the Ediacara Member fill 50–250 m canyons cut into and through the underlying unfossiliferous Chace Quartzite Member. In some places, the Ediacara Member also cuts into the underlying Bonney Sandstone (Gehling & Droser 2012). The two main fossil localities in the Flinders Ranges utilized for excavation and analysis are the National Heritage listed Ediacara fossil site at Nilpena and Ediacara Conservation Park (Fig. 1A).

These fossiliferous Ediacaran strata (Gehling 2000, Gehling & Droser 2012) represent 'snapshots' of the benthic marine communities, moulding the external and also collapsed forms of living and recently dead organisms on the base of the storm-event sands. Upward-fining sandstone event beds record current direction and waning intensity of storms (Gehling & Droser 2012). Sediment deposition was fast enough to preserve impressions of the organisms before they decayed, but gentle enough in most cases not to disturb their natural configurations. Characteristic textures are preserved on almost all fossil surfaces and suggest that the Ediacaran sea floor was covered in an organic film or mat, possibly of bacterial or algal origin (Jenkins *et al.* 1983, Gehling 1999, Seilacher *et al.* 2005, Droser *et al.* 2006). Chemical reduction of Fe and SO_4^{2-} from bacterial decay of the mat produced a pyrite/mineralized 'crust' replacing the external tissues of the organisms, and preserving communities as a hyporelief 'death mask' (Gehling 1999) on the soles of sandstone event beds (Gehling & Droser 2012). An analogous form of preservation has been described by Liu (2016) for the Mistaken Point association fossiliferous surfaces in the deeper marine Ediacaran fossil beds of southeastern Newfoundland.

Ediacara Conservation Park, where Sprigg (1947, 1949) first discovered fossils of the Ediacara biota, was originally worked for its strata-bound deposits of lead, silver and copper mineralization. Discovered in 1869, these deposits were worked until 1918 in a series of mines on the western and southern sides of the shallow Ediacara Syncline. This up-faulted outlier, on the western margins of the Flinders Ranges, consists of a thinned late Ediacaran to early Cambrian succession, extending from Beltana Station in the north, 35 km south into Nilpena Station. The low-angle tectonic

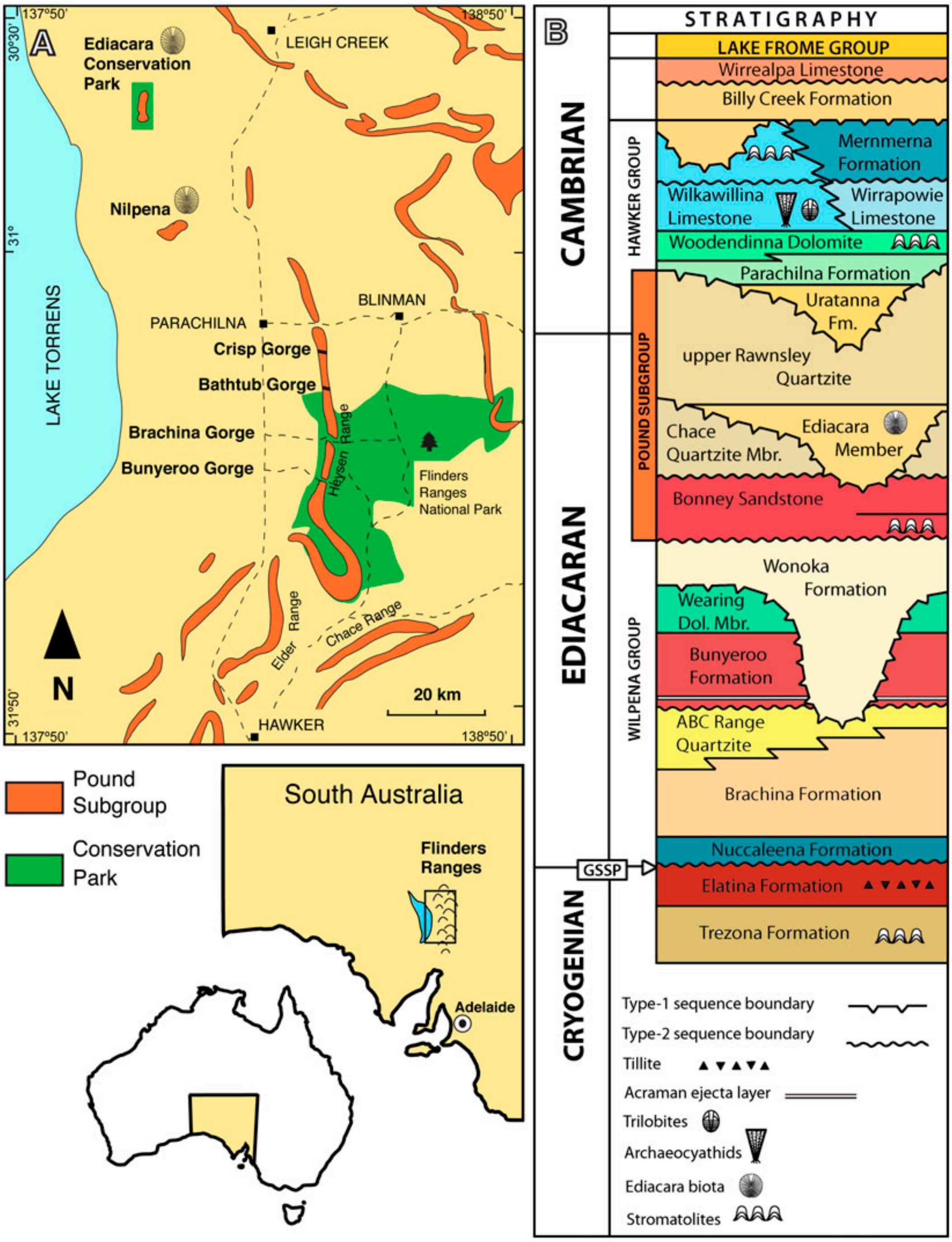

Fig. 1. **A**, Map showing the location of the Flinders Ranges within South Australia and Australia, and the fossiliferous Pound Subgroup within the Flinders Ranges (modified from Gehling & Droser 2012). **B**, Depositional sequences of the Ediacaran and Cambrian, Flinders Ranges, South Australia (modified from Gehling & Droser 2012).

structures expose outcrops of Wonoka Formation, overlain by Bonney Sandstone and Rawnsley Quartzite. At north Ediacara Conservation Park (NECP) near Greenwood Cliff, the Ediacara Member lies (immediately) below the basal Cambrian Uratanna Formation (Droser *et al*. 2006). The excavated bed (NECP Bed-1) dipping east at less than 12°, is one of a package of thin fossiliferous delta-front beds of the Ediacara Member overlain by light-coloured, coarser-grained, wave-rippled beds of the storm wave-base sand facies that thickens and coarsens upward (Gehling & Droser 2013). In this section, the shoreface sand facies of the Ediacara Member are disconformably overlain by the massive channel sand that is characteristic of the base of the Uratanna Formation. Above this truncated section of the lower Cambrian sandstones, is a 5-m-thick section of the Parachilna Formation, characterized by *Diplocraterion* burrow beds grading up into the ferruginous and manganiferous calcareous siltstones of the Woodendinna Dolomite. A N–S fault 50 m west of Greenwood Cliff repeats the upper fossiliferous facies of the Ediacara Member to the west.

An important feature of the fossil beds from the key excavation site at NECP, is that they can be matched in bed characteristics, taxonomic composition and patina, to trimmed slabs bearing type specimens of Ediacaran taxa, such as *Spriggina floundersi*, *Parvancorina minchami*, *Dickinsonia tenuis* and *Praecambridium sigillum*, which were collected without a record of exact localities in the 1950s and 1960s. In some cases, fragments of specimens collected recently have been amalgamated with incomplete specimens collected decades before. However, unrestricted collecting of large specimens from NECP since its discovery, has meant that little such material has been seen at the surface in recent decades. On the other hand, fossil specimens of many species, of less than 10 mm in size, have remained unobserved to itinerant collectors. Consequently, once key beds have been located and excavated, they can be prepared by removing underlying sand and silt laminae to reveal exquisite preservation of taxa varying from under 2 mm to more than 40 cm in maximum dimensions, thus providing evidence of orientation, spatial association and size to aid palaeoecological analysis.

Sedimentary setting

At NECP, the fossiliferous Ediacara Member represents deposition between shoreface facies and delta-front prograding deposits dissected by submarine channels. The fossil beds are 2.5–4 cm thick and consist of medium- to fine-grained feldspathic sandstones with a grainsize of 0.2–0.5 mm in diameter. Fossils are preserved on the soles of the sandstone beds mostly as negative hyporelief external moulds. Low-angle, unidirectional current ripples are preserved on the tops of the beds. Thin, discontinuous sand laminae (shims) separate the thicker fossiliferous sandstone beds. The alternating fining, upward-thinning micro-packages of sandstone, including one or more shims, is probably a result of waning storm events where sediment slurries flowed down slopes below the influence of storm waves (Gehling 1999). Microfaults are preserved as longitudinally discontinuous shallow steps (about 1–2 mm high) in the topography of the fossil surfaces; these do not hinder the analysis of fossil specimens.

Materials and methods

In this paper, we report on a well-preserved sample of an Ediacaran community, excavated from an outcrop in NECP (Fig. 1A). The sample of fossil bed, NECP Bed-1, is approximately 1.6 m² in surface area and almost every square centimetre of the bed is covered in complex organic textures or is occupied by discrete organic forms and organisms. The surface preserves some of the more commonly described taxa, which include: *Parvancorina*, *Spriggina*, *Rugoconites*, *Dickinsonia*, *Tribrachidium*, *Kimberella*, *Charniodiscus* and *Yorgia*, together with two new un-described taxa. Additionally, we briefly discuss the genera preserved on 10 smaller isolated fossiliferous slabs, which, found in the same locality as NECP Bed-1, share a similar sedimentology, taxonomic composition and Textured Organic Surfaces (TOS; see Gehling & Droser 2009). These ‘float blocks’ might have originated either directly from NECP Bed-1, or from a bed above or below. Regardless, they can be confidently placed within the same facies.

NECP Bed-1 was discovered in 2012 when a team of South Australian Museum staff and volunteers carefully excavated approximately 1.6 m² of the bed. Subsequently, another 4 m² has been excavated and is currently under preparation. The fossils are preserved on the bed sole and, as such, the process of excavation involves several steps: (1) the exposure and tracing of the bed outline onto a transparent sheet of plastic; (2) removal of the bed, which invariably comprises more than one fragment; and (3) inversion and placement of the bed onto the transparent plastic sheeting such that the fossiliferous side is facing up and the individual components are in the right configuration. The inverted and re-assembled bed then requires preparation to remove adhering laminae of sandstone and siltstone that constituted the original substrate. Preparation is facilitated by the use of high-pressure water to remove loose material, followed by small hand tools and, where necessary, by the laboratory use of vibrotools under binocular microscopes with dust extraction. In this way, the amalgamated bed is thoroughly cleaned to remove superficial silt/sand grains so as to expose the entire sole veneer that preserves the body and trace fossil moulds.

Once all component slabs had been prepared, they were amalgamated using epoxy resin and the bed was reinforced to provide structural integrity to the whole slab. Fourteen layers of rubber latex, coloured black with Indian Ink, and reinforced with cotton gauze, were used to cast the fossil beds. Care was taken with the initial coating to avoid air bubbles. The result is an accurate replication of the seafloor community after burial and before complete decay of the organisms. The latex cast is portable and amenable to labelling, allowing the spatial and size analysis of fossils. The uniform colour of the latex cast enables observation of the contours of discrete forms without the distraction of the original, in some cases, heterogeneous colour of the sandstone slabs. Low-angled lighting from a consistent direction was used for photographing the various forms on the latex cast and on the original fossil surface. Fossil moulds and latex replicas were photographed using a Canon 50D with a Canon MP-E 65 mm macro lens. Grainsize was determined using a Nikon SMZ1500 microscope with the imaging software NIS Elements.

Once all fossil taxa and other organic textures were marked on the latex, these details were traced on transparent PVC sheeting and coordinates for all discrete specimens were recorded using a 10 cm grid. Orientations of appropriate taxa were collected using a Ward's Contact Goniometer using either prescribed anterior ends or the longitudinal axis of the organisms. Locations of the organisms were measured and given an (x, y) coordinate, which were then entered into the package *Spatstat*, in the open access statistical computing software program *R*. The (x,y) coordinates of the polygonal outline of fossil beds were also recorded. Surface area measurements were calculated using *R*, and figures were made with Adobe Illustrator CS3.

Results

Collectively, this delta-front facies at NECP preserves a diverse set of body and trace fossils together with TOS. *Parvancorina minchami* (Fig. 2A) is the most common species across all studied fossil surfaces and is particularly abundant on NECP Bed-1 (Fig. 3), the largest surface (Fig. 4). The majority of the *Parvancorina* are juveniles, and have their medial ridge aligned with the prevailing palaeocurrent (352° ± 5°), as interpreted from a single, large felled specimen of the frondose *Charniodiscus* that was attached by a holdfast below the mat (Figs 2I, 3).

Several specimens of *Spriggina floundersi* Glaessner, 1958 (Fig. 2B) distributed across NECP Bed-1 (Fig. 4) appeared to have no trend in orientation. Interestingly, one specimen was preserved with only an anterior or 'head' end and half the body, with the posterior half apparently missing (Fig. 2C). Definition of its head and lateral structures were poor, suggesting that it was partly decayed or displaced at the time of burial. Apparent clusters of the tiny and possibly appendage-bearing *Praecambridium sigillum* Glaessner & Wade, 1971 were observed on numerous slabs from its type area in NECP but were absent from NECP Bed-1 (Fig. 3). *Rugoconites enigmaticus* Glaessner & Wade, 1966 (Fig. 2D), a taxon likened to extant sponges (Seilacher *et al.* 2003), was observed in similar numbers to *Spriggina* on NECP Bed-1 (Fig. 3). It is important to note that *Spriggina*, although not preserved on the float blocks observed in this study, appears regularly on other surfaces at NECP. Similarly, *Kimberella quadrata* (Fig. 2G) and *Yorgia waggoneri* (Fig. 2H) are present on NECP Bed-1 but are rare on the observed float blocks.

A single large *Dickinsonia costata* (Fig. 2E) on NECP Bed-1 was preserved with a raised region (with less relief) around its perimeter that appeared to preserve a 'ghost' of the original body's dorsal surface (Fig. 2Ea) and might evidence the contractile reaction of the organism post-burial (Gehling *et al.* 2005). The *Dickinsonia* specimen is associated with a series of faint trace fossils (impressions) of almost identical size and similar in axial orientation (Fig. 5A), previously described as *Epibaion costatus* by Ivantsov (2011) and variously described as resting or feeding traces (Gehling *et al.* 2005, Ivantsov 2011). The resting trace impressions represent the contours of the ventral side of *D. costata*, and are preserved as slight depressions in the microbial mat, whereas the body was externally moulded by the overlying bed. The fact that these 'footprints' are larger than the body fossil impression of the organism, is likely to be a function of the contractile behaviour of the organism (Gehling *et al.* 2005). Several juvenile *Parvancorina* were clustered on top of the footprints (Fig. 5Aa). Similarly, a single *Spriggina* overlies one of the two large, similar-sized, poorly preserved *Dickinsonia* footprints (Fig. 5Ba) that were created by a specimen not preserved on NECP Bed-1. Body fossils of *Dickinsonia*, are relatively rare on the surfaces studied; however, their size diversity is greater than that of any other taxon, varying from 5 to 100 mm in length.

Two moderately large specimens of *Kimberella quadrata* (Fig. 4) appeared to be associated with bulges of unknown origin at one end, which might represent chance overlap. However, given several examples of fanned sets of paired excavation marks of *Kimberichnus* (Ivantsov 2013, Gehling *et al.* 2014) preserved on this bed, these boss-like structures might represent a retracted proboscis used to make these radula-like feeding traces (Fig. 6). The external moulds of *Kimberella*, although generally aligned with the inferred burial current, are slightly asymmetric, suggesting an original relief significantly greater than most other Ediacaran body fossils. Several pellet clusters observed on the bed (Fig. 6C, D), commonly in association with *Kimberichnus*, are considered to have formed by the scraping and gathering of surficial sandy organic matter as part of the excavational feeding behaviour of *Kimberella* (Gehling *et al.* 2014).

Since the large felled specimen of *Charniodiscus* (Fig. 2I) was not overlain by any other organisms, it was likely standing erect until felled by the burial event (Fig. 4; Jenkins & Gehling 1978, Laflamme & Narbonne 2008). An incomplete frond (disc and partial stalk), preserved adjacent to the aforementioned specimen, appears to have been degraded prior to burial, providing evidence of time-averaging effects on this benthic community (Fig. 2Ic). The microbial-mat texture appears to entirely overlap this latter disc, leaving a faint definition of the marginal rim, central ring and stalk base (Fig. 7A). A third disc of approximately the same size, adjacent to the previous two, was too poorly preserved to be included in the analysis.

Almost a dozen raised 'bosses', all with a similar diameter and relief, are randomly distributed on the surface. These might be the bodies of *Coronacollina acula* (Clites *et al.* 2012); however, the lack of associated impressions of long, thin spicular structures prevents unequivocal identification. Large, diffuse fusiform bodies, vaguely resembling frond-like organisms, were observed with no apparent preferred orientation, and suggest a cryptic history of decay of earlier living

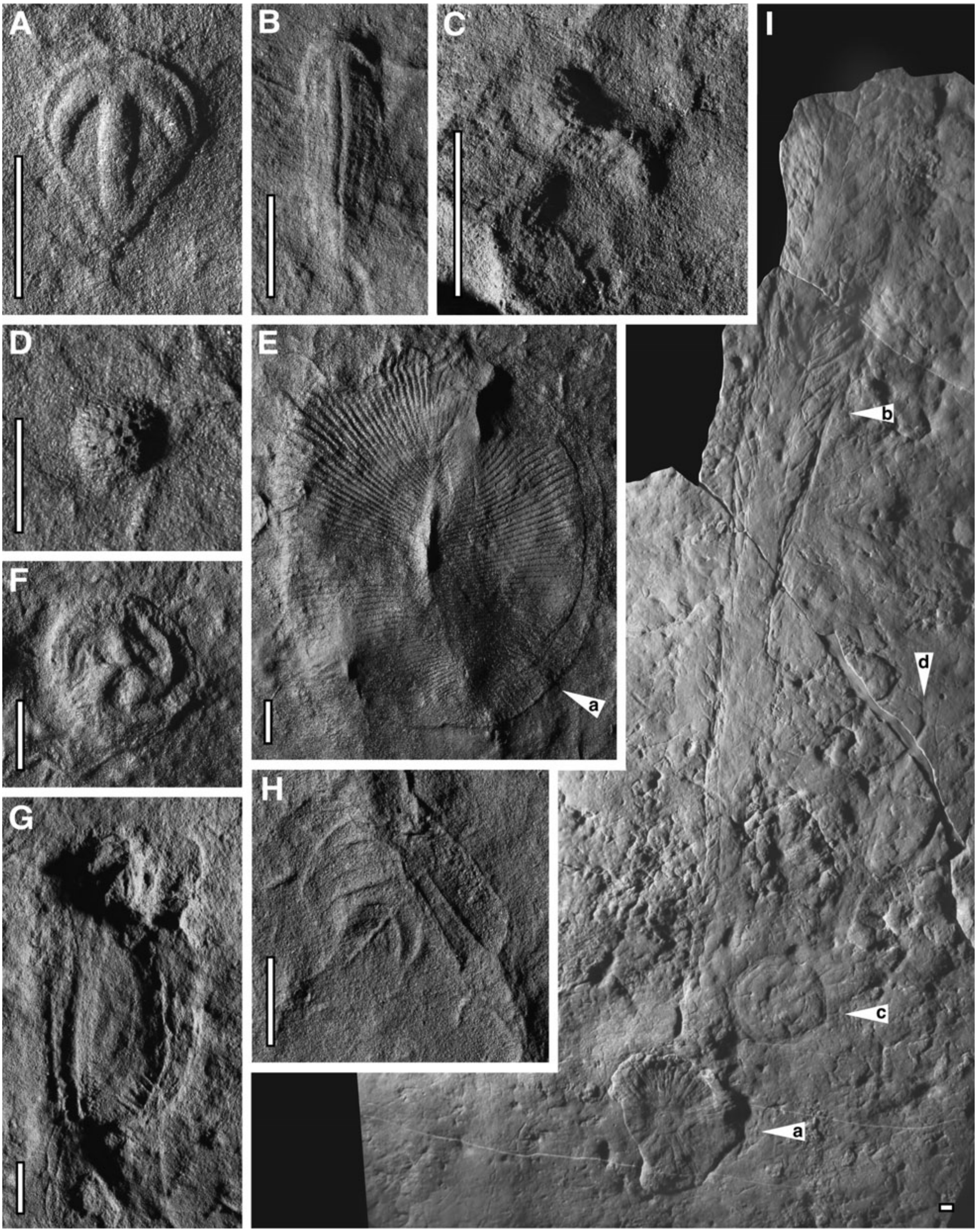

Fig. 2. Taxa observed on NECP Bed-1. **A**, *Parvancorina minchami*, SAM P49380. **B**, *Spriggina floundersi*, SAM P49389. **C**, Partially preserved *Spriggina floundersi*, specimen unregistered. **D**, *Rugoconites enigmaticus*, SAM P49388. **E**, *Dickinsonia costata* and (a) peripheral rim, SAM P49377. **F**, *Tribrachidium heraldicum*, SAM P49372. **G**, *Kimberella quadrata*, SAM P49391. **H**, *Yorgia waggoneri*, SAM P49365. **I**, *Charniodiscus* (a) holdfast and (b) primary modules, SAM P49366; poorly preserved *Arborea*, (c) holdfast and (d) terminally folded stalk, SAM P49386. All photos taken from the latex cast, except H, which is of the original fossil bed. Scale bars = 1 cm.

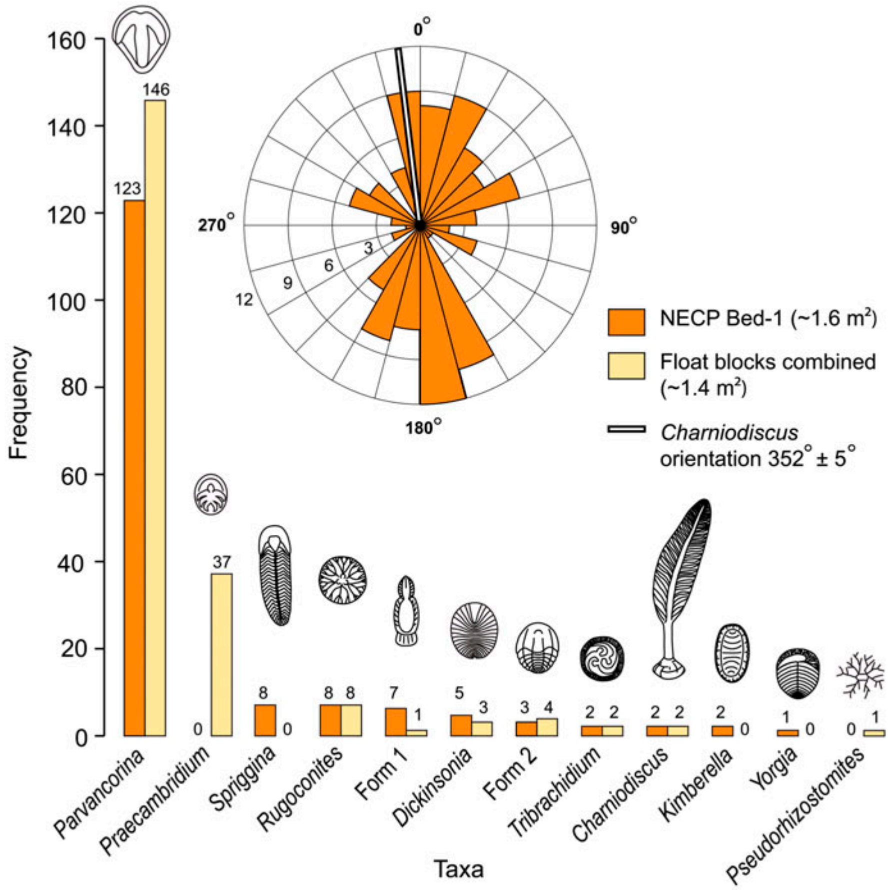

Fig. 3. Histogram showing the abundances of the recorded taxa and rose diagram showing the relative orientations of *Parvancorina* specimens on NECP Bed-1. The numbers 3, 6, 9, 12 in the rose diagram represent frequency bins, and the white rectangle indicates the orientation of the *Charniodiscus* and estimated burial current.

organisms on NECP Bed-1, well before the burial event. Descriptions are in preparation for two new diminutive but distinct taxa, observed on the NECP surfaces (i.e., Form 1 and Form 2; see Fig. 3).

Discussion

Taphonomy

The fossil assemblages from extensive serial excavations of more than 30 beds at Nilpena were originally considered to be ‘snapshots’ of exclusively living benthic assemblages of the Ediacara biota. However, the role of the organic-rich mats consisting of both accumulated bacterial mats and matted body fossils has been emphasized recently (Gehling & Droser 2009, Xiao *et al*. 2013). Here, we propose that the community preserved on NECP Bed-1 was relatively mature; and the character of the TOS and the presence of some apparently poorly preserved fossils suggest a form of time-averaging, with the assemblage consisting of both living and dead organisms at the time of burial. The concept of ‘effaced preservation’ of particular soft-bodied Ediacaran organisms was proposed by Liu *et al*. (2011) in reference to older Avalonian assemblages, where irregularly shaped forms with inconsistent textures among perfectly preserved fronds were observed, and Liu *et al*. (2011) argued that the former were effaced fronds partially decomposed by digestive microbial activity, prior to burial. Gehling & Droser (2013) suggested that the amount of preserved TOS corresponds to the time lapsed between sedimentation events. However, when assessing the community structure of Ediacaran assemblages, clearly species counts need to be limited to organisms that were alive at the time of burial. Unlike Phanerozoic examples of time-averaged fossil assemblages, which can consist of bioturbated substrata and extensively transported organisms, the Ediacara biota are preserved as complete *in situ* benthic marine communities, a phenomenon unknown in the Phanerozoic. Ediacaran fossil beds contain all the elements of a complex community, including dead and decomposing organisms among those that were alive and active immediately before the burial event. Kidwell & Bosence (1991) used the term ‘census assemblage’ to describe a form of time-averaging among Phanerozoic fossil assemblages that were preserved within the same temporal setting. However, their description of a census assemblage also included deceased organisms owing to unique environmental conditions preventing the decay and decomposition of carcasses. In contrast, Ediacaran communities clearly

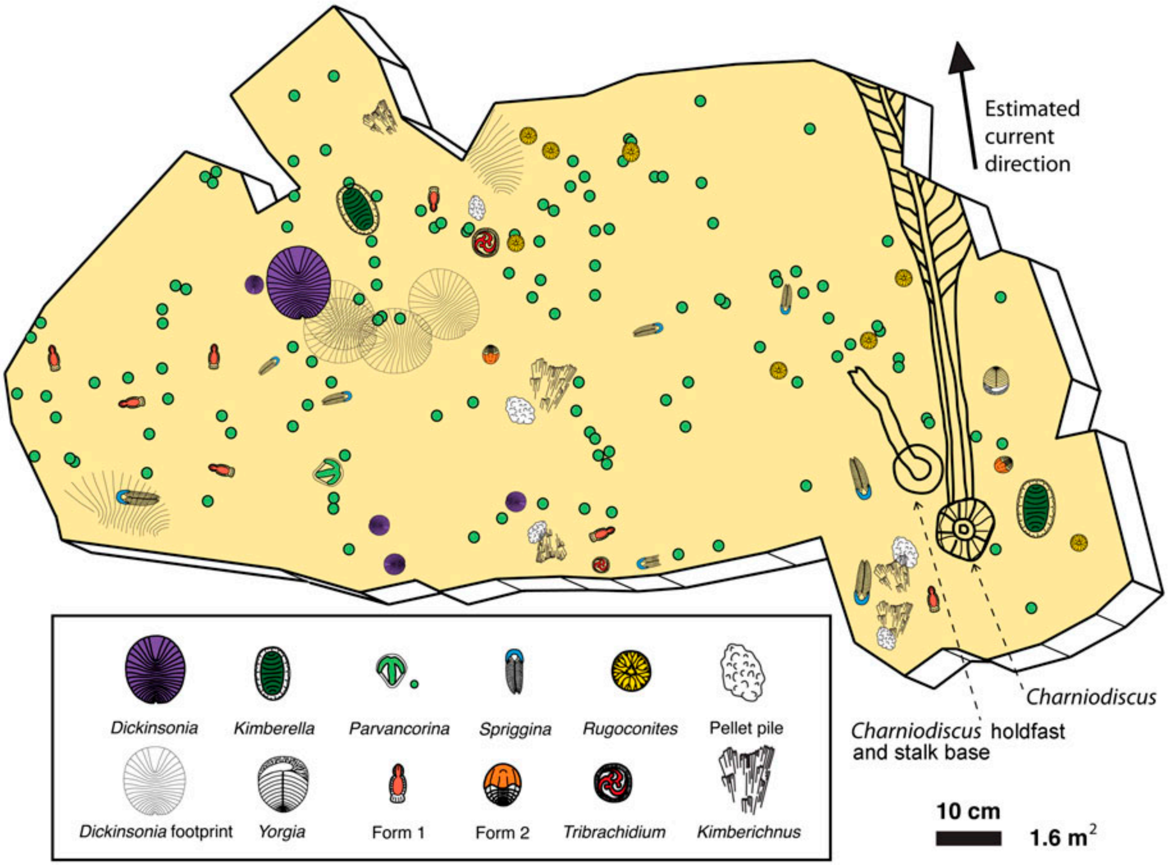

Fig. 4. Illustration of NECP Bed-1 showing the relative positions of the taxa on its surface. Sizes of illustrations are approximately relative; however, the smaller taxa (i.e., *Spriggina*, *Rugoconites*, juvenile *Parvancorina* and *Dickinsonia*, Form 1 and Form 2, are larger in this diagram than in reality for visual purposes. The illustration depicts the orientation of the individuals in the community, instead of the inverse fossil sandstone bed.

involve an element of time-averaging owing to the unique preservation of all forms of soft bodies including both vital and deceased macro-organisms together with the background microbial mats that supported them. No longer can we make the assumption that all Ediacaran communities were simply snapshots of the living biota at the time of burial.

The fossil communities preserved on NECP Bed-1 and float slabs from NECP appear more complex than Ediacaran surfaces from other well-studied Flinders Ranges localities. At Nilpena, studies of more than 30 excavated fossil beds have revealed major differences in density, diversity and evenness in the distributions of organisms. Like NECP, this is evidenced by the preservation of topographically complex and highly concentrated TOS, trace fossils, and the preservation of what appear to be partially decayed organisms (Droser *et al.* 2006, Gehling & Droser 2009). However, the main difference between these localities is that the excavated beds from NECP feature much finer sand moulding the sole surfaces, reflecting deeper-water, delta-front settings. In comparison, most of the excavated beds at Nilpena are from storm wave-base settings where sand is medium- to relatively coarse-grained and more feldspathic. Consequently, the TOS are limited to relatively large-scale wrinkles, pucker marks and felled specimens of *Funisia* at Nilpena (Droser & Gehling 2008, Gehling & Droser 2009).

Unravelling the relationships between living macro-organisms and those that might have been dead well before the burial event involves interpretation of the time elapsed since recruitment and the ambient conditions responsible for the assemblage preserved. The orientation of *Charniodiscus* and juvenile specimens of *Parvancorina* (Fig. 3) suggests that they were involuntarily aligned with the current involved in the burial event. However, the assumption that the *Charniodiscus* was felled by the burial current does not necessarily mean that *Parvancorina* were also oriented by the same burial current, and instead *Parvancorina* might have previously been axially oriented parallel to a prevailing ambient current. Given the diminutive size of most specimens, it is unlikely that alignment was involuntary and purely hydrodynamic, since these specimens would have been within the critical boundary layer of any bottom current. The issue of whether the orientation of diminutive specimens of *Parvancorina* (<4 mm long) was a response to ambient current flow or due only to the burial event requires a broader study of community samples from several beds and environmental settings. The fact that the majority of the individuals are juveniles and all of a similar size, might indicate a common

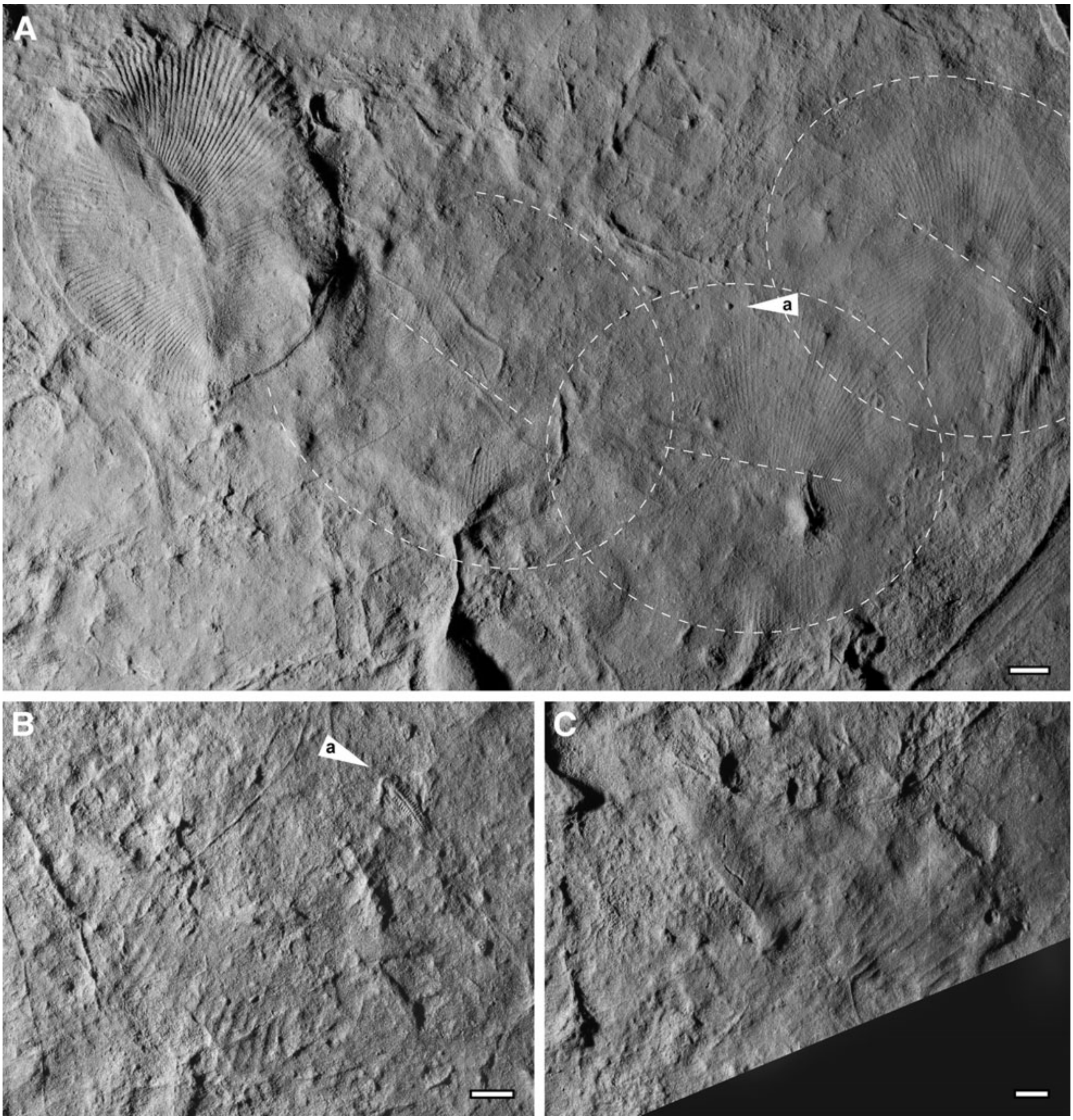

Fig. 5. Dickinsonia trace fossils on NECP Bed-1. **A**, Series of at least three footprints trailing behind the body impression, SAM P49377, and (a) cluster of juvenile *Parvancorina* overlapping the footprints. **B**, Poorly preserved footprint of a larger individual and (a) *Spriggina* specimen overlapping the footprint. **C**, Poorly preserved footprint of a larger individual. The footprints in B and C were created by one or more large individuals indicated by the longitudinally larger segments, body fossils of which were not preserved on NECP Bed-1. All photos taken of the latex cast. Scale bars = 1 cm.

reproductive origin (Droser & Gehling 2008). However, future multi-surface analyses of size and spatial association will be necessary to confidently invoke any reproductive implications.

Diversity as a function of resolution

Although the surface area of NECP Bed-1 described here is less than 2 m², the taxonomic diversity (10 genera) is high relative to equivalent areas of fossil-bearing surfaces from the Flinders Ranges and equivalent localities globally. For instance, a diversity of 2–14 taxa per fossil bed occurs in numerous cases from South Australia (Droser & Gehling 2015), and a diversity of 1–13 taxa has been described from the fossiliferous White Sea locality in Russia (Grazhdankin 2004, Bottjer & Clapham 2006, Zakrevskaya 2014). Furthermore, relatively large slabs collected from subcrop near the excavation site for NECP Bed-1 also have a similar taxonomic diversity. Our initial investigations, therefore, suggest that the fossil bed at NECP bears some of the greatest faunal densities among

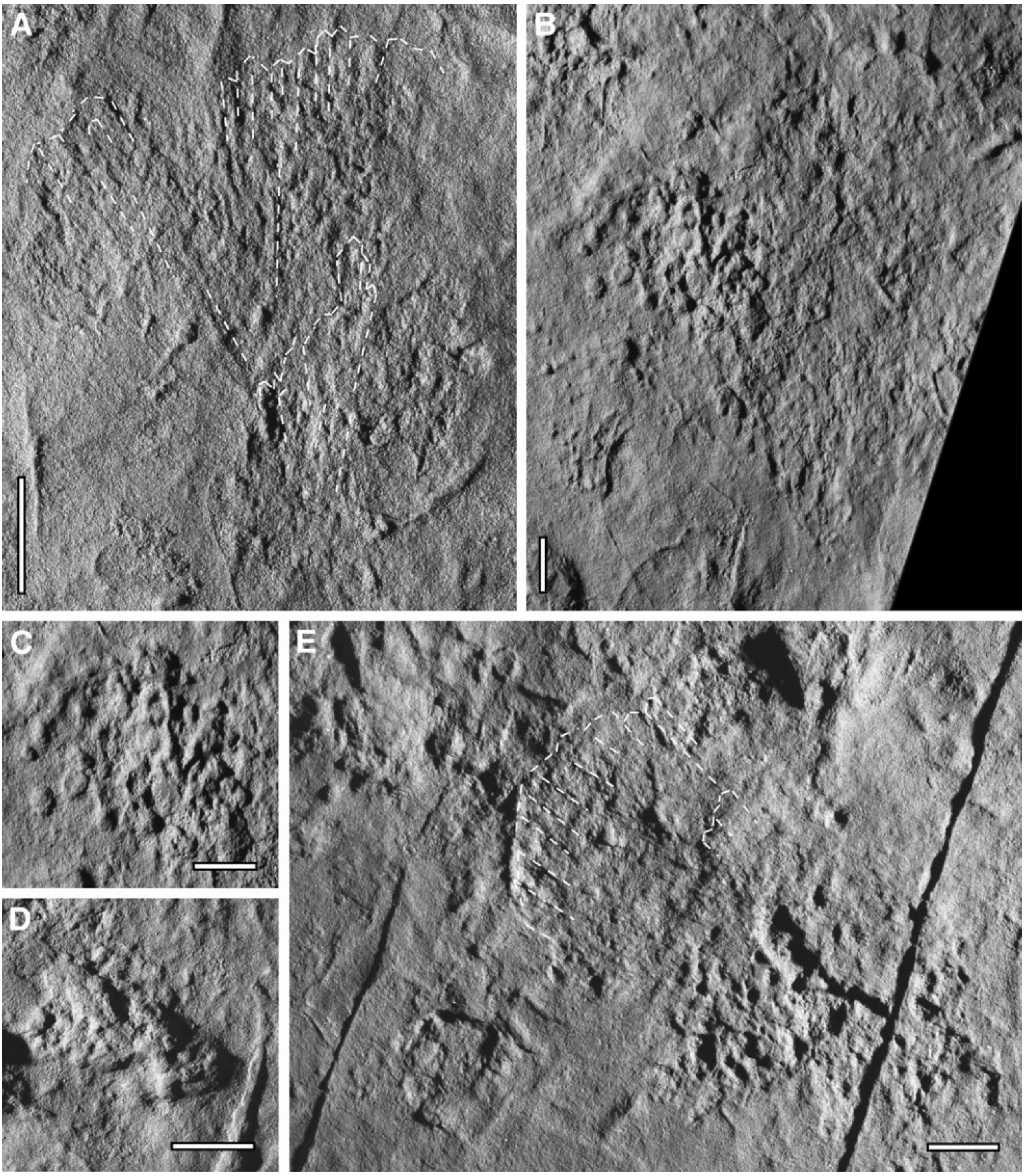

Fig. 6. Kimberella feeding traces (*Kimberichnus*) and piles of accumulated sediment/organic matter. **A**, Typical fan-shaped trace fossil, SAM P53895. **B**, *Kimberichnus* and pellet pile, SAM P53896. **C**, Enlargement of pellet pile from B. **D**, Pellet pile, *Kimberichnus* not preserved. **E**, *Kimberichnus* and a partially developed pellet pile, SAM P53897. All photos taken of the latex cast. Scale bars = 1 cm.

equivalent localities in the Flinders Ranges and similar to that recorded from the White Sea of Russia; highlighting the importance of continued research at this locality.

The sand grains moulding NECP Bed-1 are comparably fine and, because the level of observed detail increases with a smaller grainsize, the fossils are preserved with a relatively high resolution. Additionally, the prominence of TOS may help to account for the quality and detail of body fossil specimens preserved on NECP Bed-1. The two new taxa discovered on these NECP beds (Form 1 and Form 2) have not been observed at any other Ediacaran locality in the Flinders Ranges. This may be a matter of resolution, since both forms are less than 11 mm in maximum dimension, their confinement to NECP beds may be due to the res-

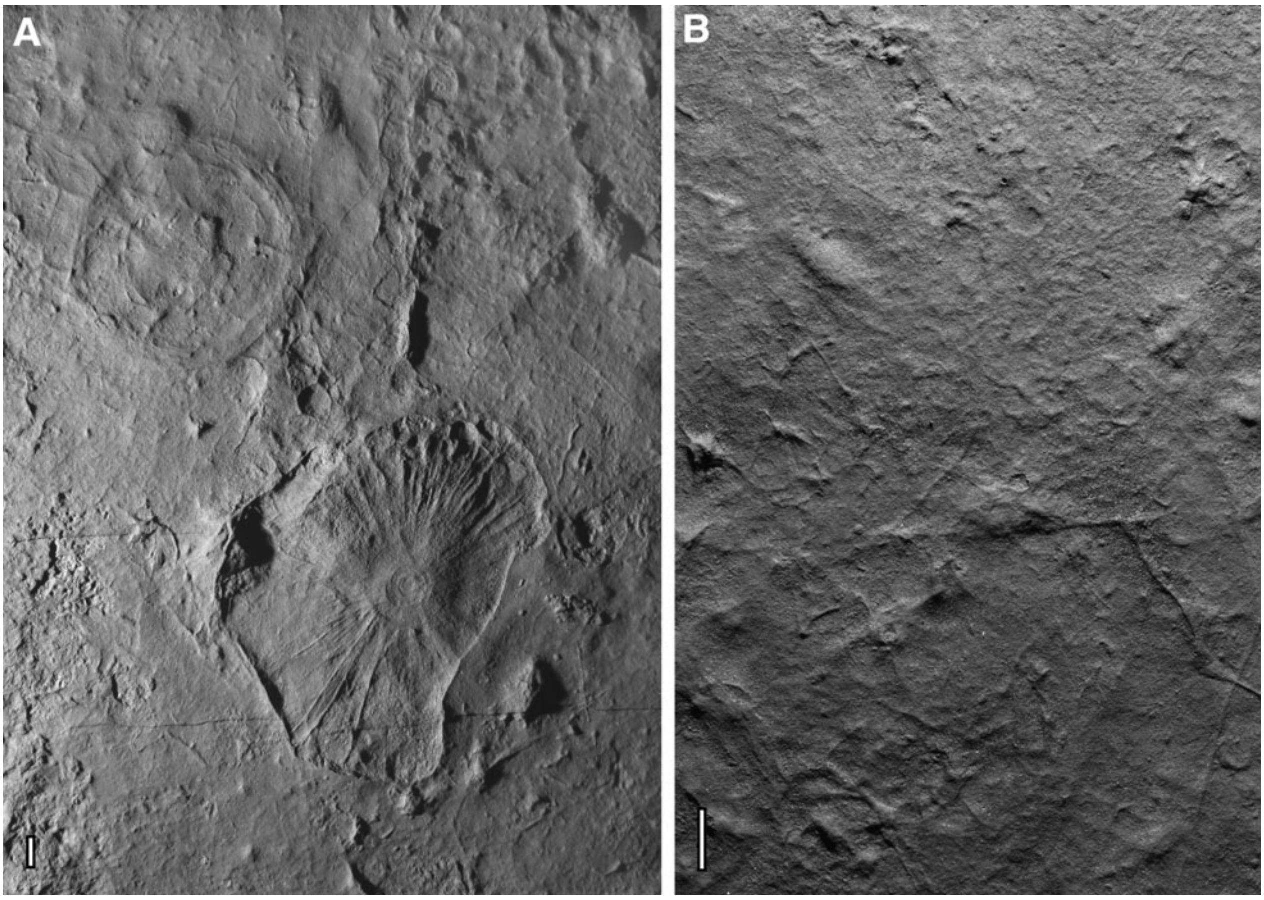

Fig. 7. **A**, Holdfast disc of large *Charniodiscus* (bottom), SAM P49366, holdfast disc of poorly preserved *Charniodiscus* (top left). **B**, Sample of textured organic surface. All photos taken of the latex cast. Scale bars = 1 cm.

olution provided by the sediment grainsize. As a comparison, juvenile *Parvancorina*, although abundant on NECP bedding surfaces, may only be recognizable as small undifferentiated bumps on coarser-grained Nilpena beds. Likewise, *Praecambridium*, which is never longer than 6 mm, is largely restricted to NECP from the same package of beds described herein. In the absence of evidence for differences in age and environmental setting, it is apparent that the key factor accounting for the high diversity of diminutive members of the Ediacara biota is the fine grainsize of the NECP beds.

Niche diversity and succession

Ecological tiering has been proposed as a means of sustainable niche occupation among older Ediacaran assemblages (Clapham & Narbonne 2002, Laflamme & Narbonne 2008). In the White Sea association (South Australia), the presence of defined tiering is less obvious, as most organisms tend to be low-lying epifauna and complete frond-like organisms, such as *Charniodiscus*, tend to be less prominent. However, Bottjer & Clapham (2006) have suggested that White Sea communities incorporate two tiers. That is, the grazers (i.e., *Dickinsonia*, *Kimberella* and *Yorgia*) and presumed suspension feeders (i.e., *Rugoconites* and *Tribrachidium*; Rahman *et al*. 2015) comprise the basal tier, whereas ‘fronds’, such as *Charniodiscus* (also suggested to be suspension feeders), comprise the upper tier. This implies that NECP Bed-1 hosted a rich diversity of grazers and suspension feeders, which were actively exploiting benthic and suspended sources of food respectively. Apparent sessile organisms, such as *Tribrachidium*, might have utilized their distinctive three-armed topology to slow currents bearing food particles as an aid to filter feeding (Rahman *et al*. 2015). The feeding mode of *Spriggina* and *Parvancorina* has yet to be assessed with any confidence. A third tier, that of mat-burrowing, was proposed by Seilacher (1999) as ‘undermat mining’. It is now apparent that *Helminthoidichnites* groove traces represent both surface mining of mats and also burrowing after shallow burial. Furthermore, these cryptic burrowers were also targeting recently buried organisms (Gehling *et al*., pers. obs.).

It has been suggested that a limited number of eco-spaces or modes of life were occupied by organisms during the Ediacaran Period with the potential for the occupation of more (Bambach *et al*. 2007). This is largely a consequence of the taphonomy of Ediacaran fossils, which limits the potential of known synecologies (fossil bed fragmentation and poor preservation being the major contributors). Although taphonomic limitations are present, there is still a significant amount of palaeoenvironmental information preserved, such as spatial arrangement and morphology. Morphological diversity has been linked to the functional environment with which an organism interacts (Bambach *et al.* 2007), and the diverse morphologies observed on NECP Bed-1 might, therefore, be indicative of a complex palaeoenvironment, hosting various sources of nutrition for its occupants; whether it was through suspended nutrients in the water column or benthic sources.

In modern communities, it has been demonstrated that the diversity of marine invertebrate communities parallels the complexity of the algal mats with which they interact (Dean & Connell 1987). Through observations of an intertidal region in Southern California and laboratory experiments, Dean & Connell (1987) demonstrated that in a modern community, greater biomass and surface area of algal mats were directly correlated with marine invertebrate diversity. Half a billion years earlier, the sample Ediacaran community living on NECP Bed-1 might have demonstrated a similar pattern, where greater organismal diversity corresponded to the apparent complexity of the microbial mat. Furthermore, the same link between microbial mat complexity and organismal diversity has been observed at other Ediacaran fossil localities (Liu *et al.* 2011).

In addition to dead and decaying organisms, NECP Bed-1 preserved organisms that were clearly at different stages of growth, consistent with a developing complex community (Dean & Connell 1987, McCann 2000, Naeem 2001). For instance, the large holdfast-attached *Charniodiscus* frond, at more than 50 cm long, had clearly occupied its sedentary position for a significant interval. This alone demonstrates that the entire community had developed within the same interval, before the burial event. The presence of the two *Charniodiscus*, each of decreasing preservational integrity might indicate a common origin, and is perhaps indicative of succession, or reproductive strategies (Clapham *et al.* 2003).

In fossil and extant marine communities, early succession is characterized by low species diversity and low evenness; mid-succession by high species diversity, high evenness and tiering; and late-succession by both lower species diversity and evenness (Sousa 1980, Vance 1988, Clapham *et al.* 2003). First, we can negate the probability of NECP Bed-1 being an early successional community owing to the relatively high species diversity, and the relatively balanced coexistence of both adult and juvenile organisms; except for the cohort of juvenile *Parvancorina*. Second, the species evenness appears to be too low to represent an example of a stable mid-successional community, although the diversity is relatively high; hence, a mid-stage successional affinity is equivocal. However, the relatively high species diversity and low evenness appear to be most parsimoniously explained by a late-successional community. Late-successional communities also tend to contain rare species (Sousa 1980); demonstrated here by the presence of a single *Yorgia*, which is scarce on Ediacaran surfaces. Furthermore, the presence of large fronds in Ediacaran communities has also been linked to late-stage succession (Clapham *et al.* 2003). The community structure preserved on NECP Bed-1 appears to reflect that of modern communities (Hughes 1984, 1986), where, within the community a few abundant species (*Parvancorina*), and an increasing number of rarer species were present (i.e., *Kimberella* and *Yorgia*). This trend appears to have occurred relatively frequently among Ediacaran communities (Clapham *et al.* 2003, Droser & Gehling 2015, Hall *et al.* 2015).

Trace fossils

Trace fossils are important markers of evolutionary innovations in the history of life (Erwin *et al.* 2011), such as movement (Liu *et al.* 2010, Droser *et al.* 2014, Droser & Gehling 2015), feeding (Sperling & Vinther 2010, Ivantsov 2013, Gehling *et al.* 2014) and competition (Clapham & Narbonne 2002, Clapham *et al.* 2003, Laflamme & Narbonne 2008). The orientations of the footprints and the final resting position of the large *Dickinsonia* specimen on NECP Bed-1 indicate that the organism was capable of movement across the seafloor (Glaessner & Wade 1966, Runnegar 1982, Evans *et al.* 2015). The observation that these footprints do not always become more pronounced the closer to the source, having inconsistent definition and depth, suggests that the resolution of the footprints is a possible method of assessing the time lapsed between movement of these 'mat animals' from one resting site to another. This is consistent with the hypothesis that *Dickinsonia* moved from one site to another on the mat, passively decomposed the mat (Ivantsov & Malakhovskaya 2002), and absorbed the nutrients via its basal epiderm Gehling *et al.* 2005, Fedonkin *et al.* 2007, Sperling & Vinther 2010). Additionally, the preservation of *Parvancorina* and *Spriggina* moulds overlapping the dickinsoniid trace fossils is a means of assessing the relative time lapse between the creation of the traces, and the movement of the individuals over the footprints. The preservation of partial, but larger dickinsoniid traces demonstrates that other individuals occupied the surface before it was smothered, where such old 'footprints' are either degraded, or overlain by freshly moulded organisms (Fig. 5Ba). Such observations enable a degree of time resolution for the total preserved assemblage.

Dickinsonia, *Yorgia* and *Kimberella* are the only known genera of macrofossils that have left traces of feeding activity or locomotion in the Ediacaran. The explanation lies in the fact that trace makers had to be capable of disrupting or ploughing the substrate mats or degrading these mats in order to leave a record of their locomotive or feeding behaviour. Small specimens of *Kimberella*, preserved with an extended proboscis (Gehling *et al.* 2005), are associated with fanned sets of

Kimberichnus excavation traces. Through this action, the organism actively disturbed the substrate and significantly altered the topography of the surface. Unless the feeding behaviour of an animal resulted in disruption of the mat or sediment surface, it left no visible evidence of locomotion. The absence of trace fossils created by many Ediacaran genera might be a direct result of the living microbial mat, continuously overgrowing and correcting faunally induced 'damage'. In support of this hypothesis, we observed examples preserved on NECP Bed-1, of trace fossils created some time before the burial event that were partially degraded and appear almost 'overgrown' with microbial mat.

Obstacles and future research directions

It is important to recognize that NECP Bed-1 is a sample of an Ediacaran community, and the actual spatial extent to which the community interacted is unknown. Modern marine communities have patchy distributions, and are difficult to assess owing to the obstacle of the submarine environment and the dynamics of living organisms. Therefore, we have the advantage of analysing static fossil communities. However, we face two major taphonomic obstacles, grainsize and fossil bed contiguousness. The fine grainsize moulding NECP Bed-1, and adequate surface area make it a good example for palaeoecological analyses, and by excavating more of this particular bed we may improve our understanding of the community and the complex behaviours that these organisms displayed. Future studies will benefit from the excavation and preparation of a suite of beds from the site, and a particular focus on distinctive and globally significant genera, such as *Parvancorina*, *Tribrachidium* and *Dickinsonia*, would be beneficial in resolving issues of palaeogeography and biostratigraphic ranges for which there is currently little knowledge. Palaeoecological analysis of these surfaces, which preserve some of the smallest known Ediacaran specimens in large numbers, is in progress.

Conclusions

Seventy years after the discovery of Ediacaran fossils by the late Reginald Sprigg (1947, 1949), the first excavation of fossil beds from the northern end of Ediacara Conservation Park has revealed an unexpected level of new information of an Ediacaran community and, hence, one of the earliest shallow benthic marine animal communities on Earth. The fine grainsize preserving the community on NECP Bed-1 provides a high degree of resolution, enabling the visualization of millimetric-scale organisms including an abundance of juvenile *Parvancorina*, and two new taxa. The complex TOS characteristic of fossil beds from NECP are more developed than those evident at other sites in the Flinders Ranges. In conjunction with the high generic diversity and trace fossils, these surfaces are indicative of limited time-averaging and a community at late-stage succession. The high diversity, abundance of organisms and extensive trace fossils suggest that the microbial mat community on NECP Bed-1 provided plentiful resources for its occupants. Furthermore, these characteristics suggest significant and perhaps seasonal intervals between burial events, allowing the development of mature benthic communities.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Chapter 3

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

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Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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

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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.

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 communities could have important 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

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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 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 could 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 ≈ 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 m^2 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 relative to the 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). More than 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 μm) with rarer large sand grains and ferruginous, millimeter-thick silt, to fine-grained sand partings between more coherent sandstone beds.

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

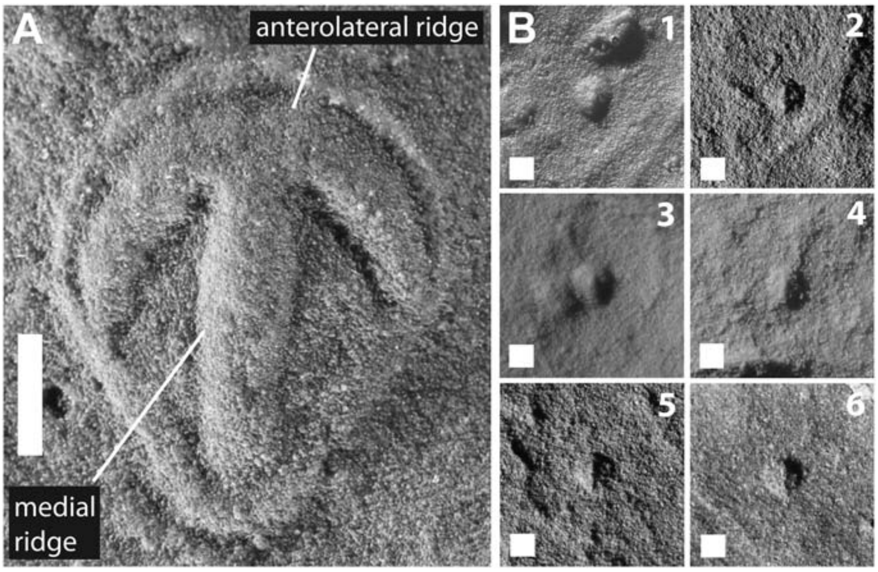

Fig. 1. Juvenile *Parvancorina* had a more pronounced medial ridge. A. Largest specimen of *Parvancorina minchami* on North Ediacara Conservation Park (NECP) Bed-1, SAM P49380 (South Australian Museum specimen identification number); B. Juvenile *Parvancorina minchami* observed on NECP Bed-1 and float 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.

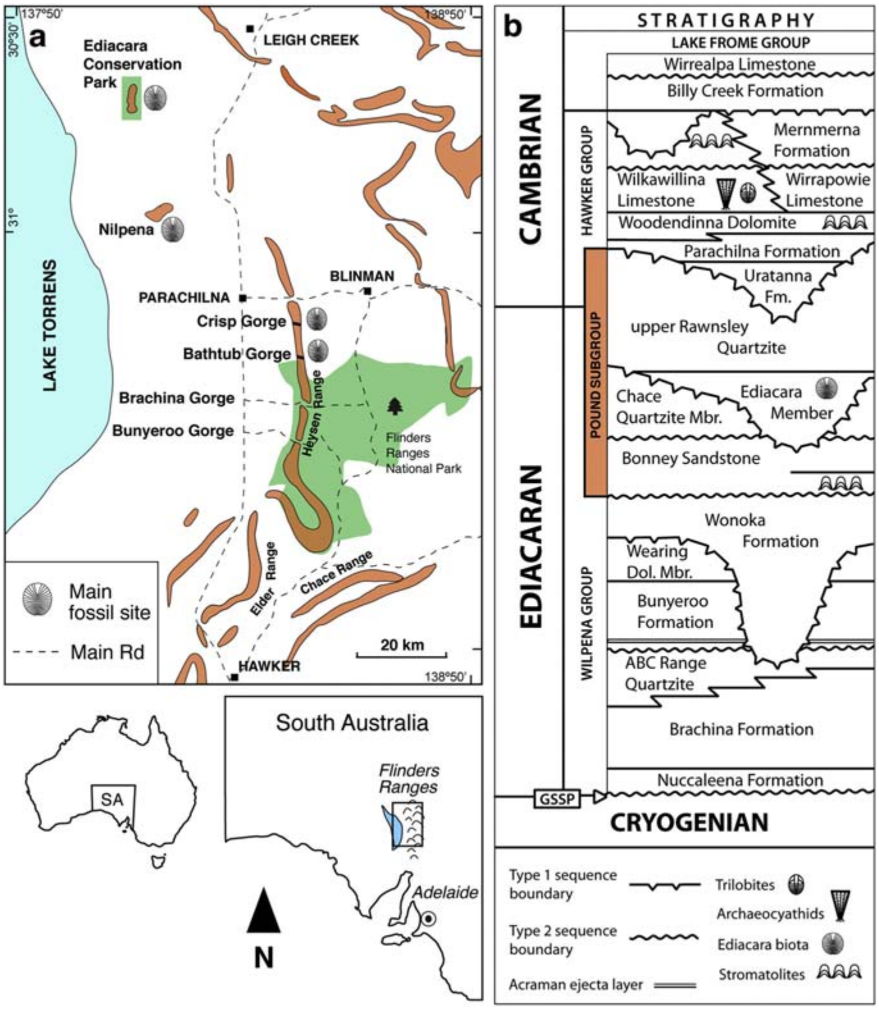

Fig. 2. Fossiliferous Ediacaran outcrop in the Flinders Ranges, South Australia. A. Map highlighting (orange) the outcrop of the Pound Subgroup containing the fossil-bearing Ediacara Member in the Flinders Ranges, South Australia. B. Generalized stratigraphic succession of the Cryogenian-Ediacaran-Cambrian 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).

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 m^2 (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 clustering 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 pairwise 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 test for 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).

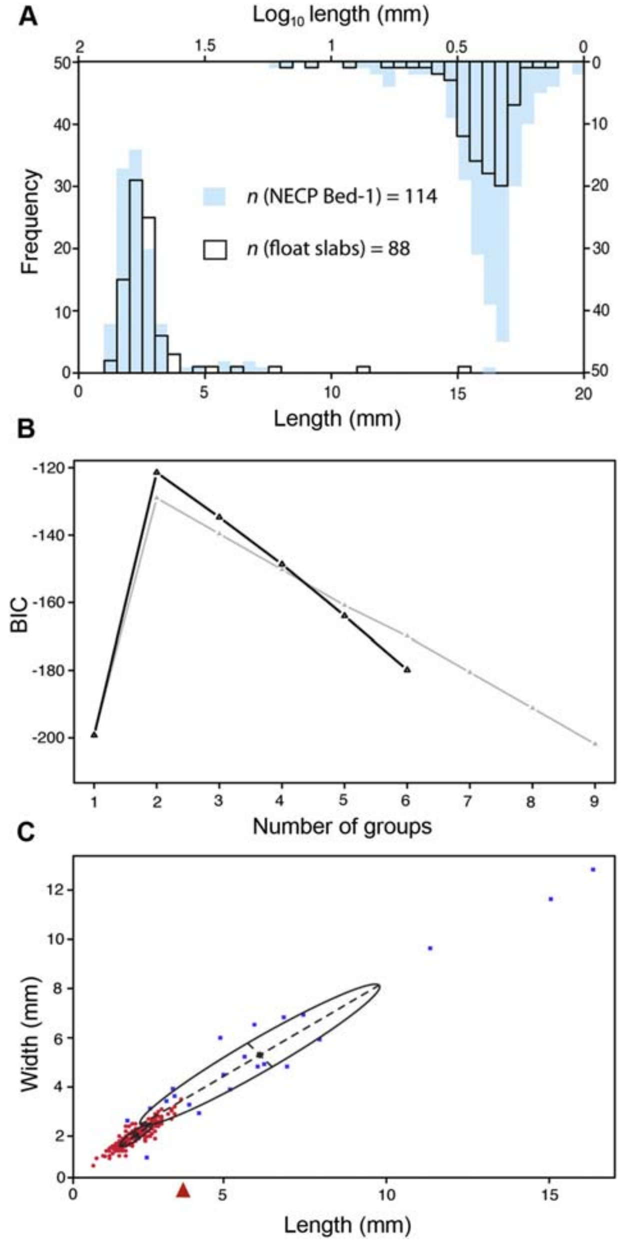

Fig. 3. NECP Bed-1 comprised a juvenile-dominated population, and two distinct size groups were present. A. Linear (bottom) and log-transformed (top) size frequency of length (in mm) of *Parvancorina* from North Ediacara Conservation Park (NECP) Bed-1 (blue fill, $n = 114$) and from the combined float slabs (black border, $n = 88$). Median *Parvancorina* length 2.3 ± 1.7 (SD) mm among specimens on NECP Bed1 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 < 4 mm in length, distinct from those > 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.)

4.1. Two size classes are identified

We found 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

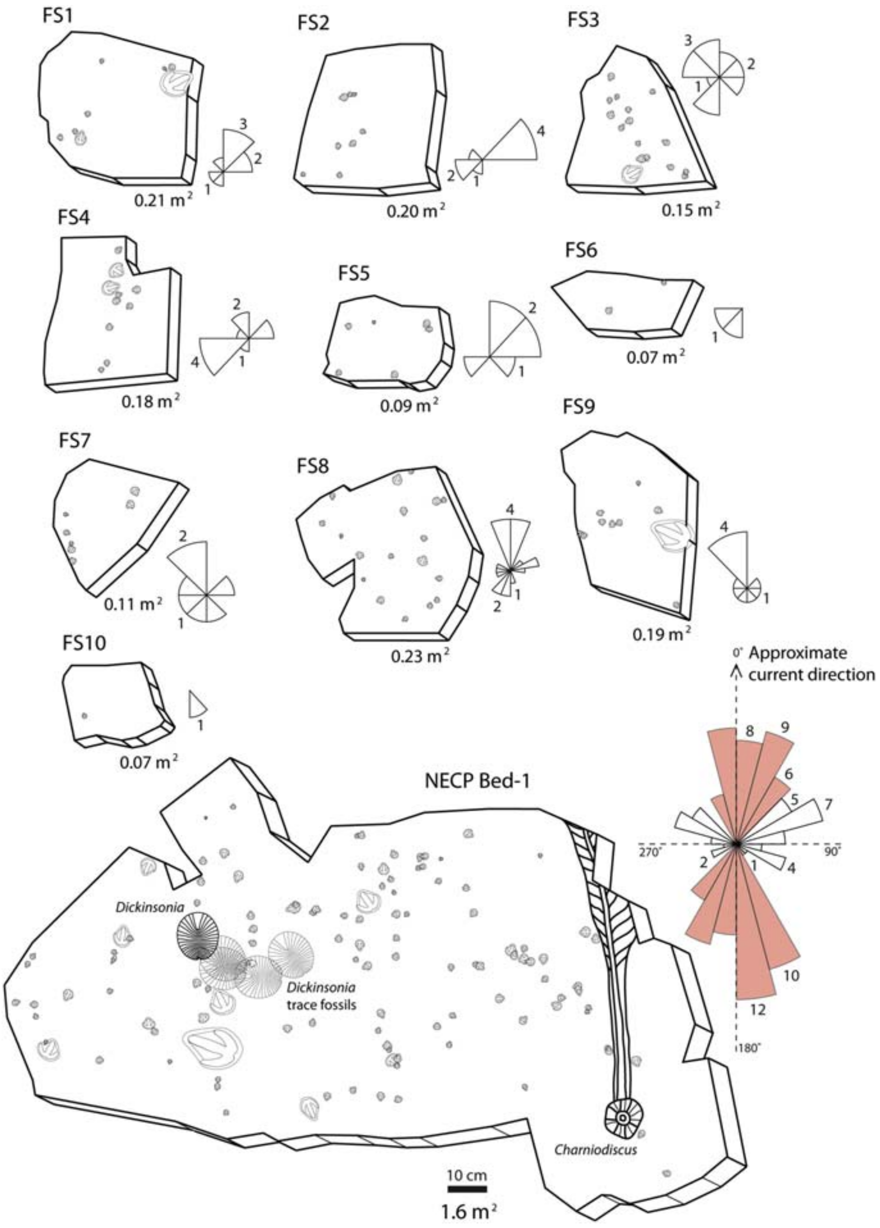

Fig. 4. Distribution of *Parvancorina* on the fossil seafloor. Spatial distribution of *Parvancorina* on North Ediacara Conservation Park (NECP) Bed-1 and float slabs, with relative orientations. The rose diagram of the specimens on NECP Bed-1 shows a strong bimodal bias in orientation (bottom right), 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.)

orientation (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 dominant 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. 5F). *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 ~ 1.5 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).

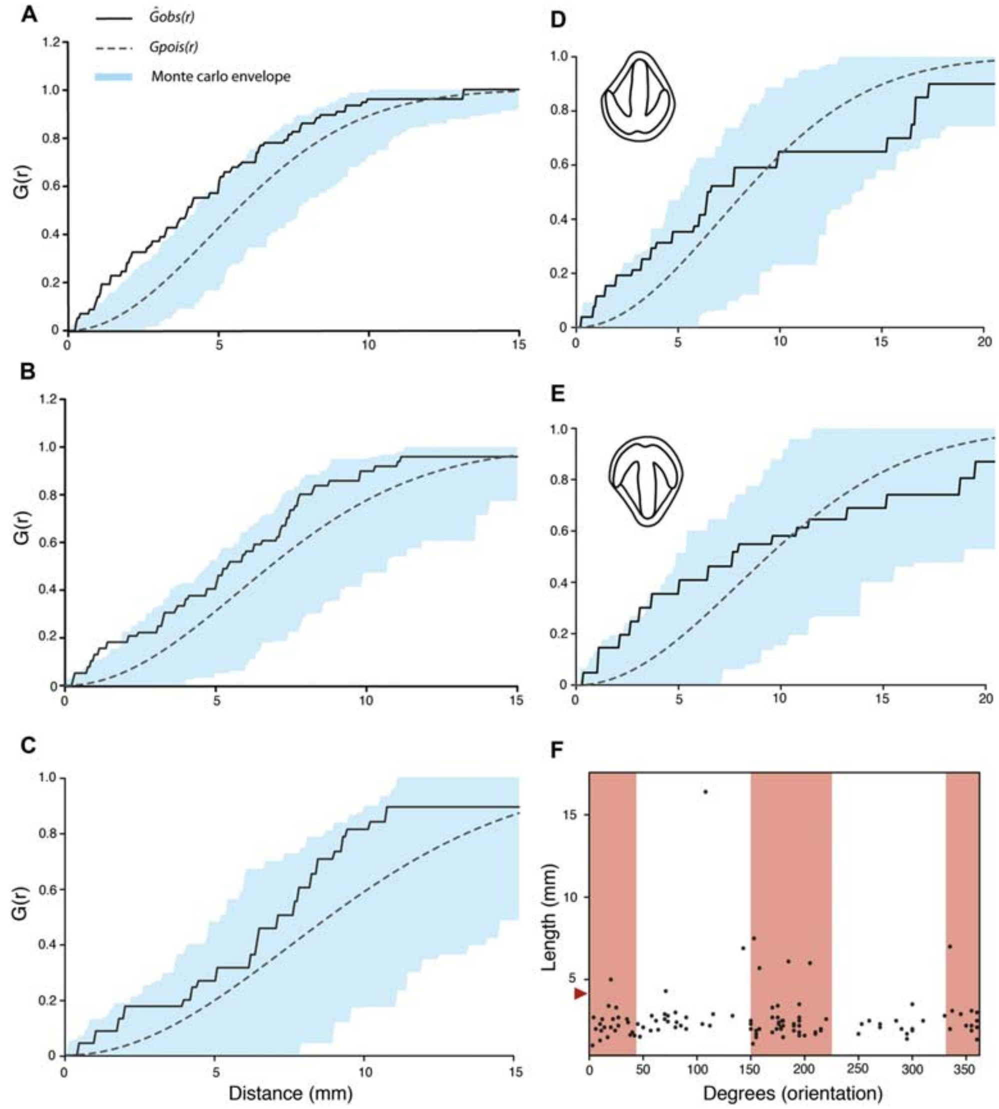

Fig. 5. Juvenile *Parvancorina* demonstrated spatial aggregation. A. Nearest-neighbor cluster analysis of *Parvancorina* on NECP Bed-1 shows that the specimens are spatially aggregated. Values of $\hat{G}_{obs}(r) > G_{Pois}(r)$ indicate a clustered spatial distribution while $\hat{G}_{obs}(r) \approx G_{Pois}(r)$ 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 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 < 4 mm in length (first size group demonstrated in Fig. 4) distinct from those > 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.)

To test for aggregation between pairs of points, the pairwise-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 pairwise 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 evidence for two size classes satisfies 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 might demonstrate more accurately the dorsal morphology of *Parvancorina*, at that stage. The morphological differences observed between the two size classes therefore support our second hypothesis.

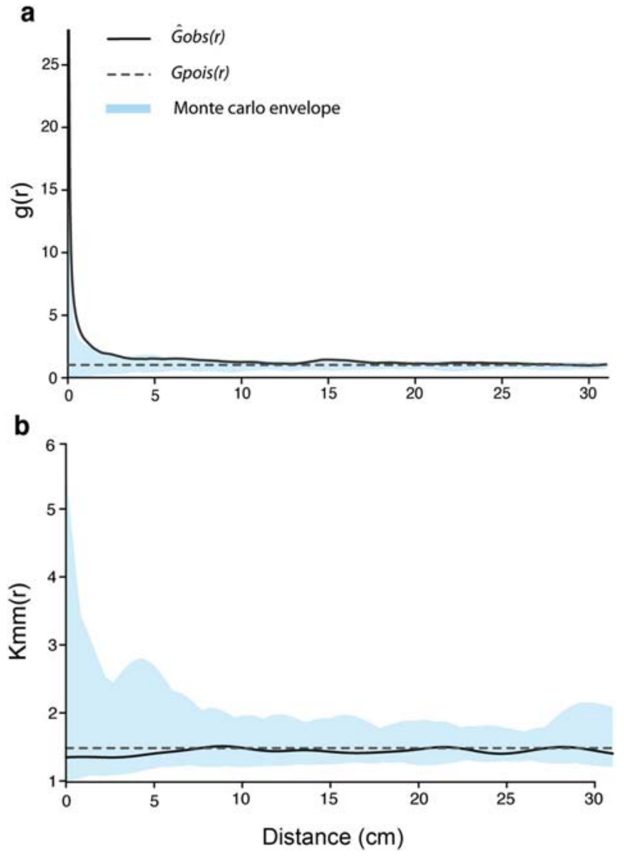

Fig. 6. Pairwise associations, and no association between inter-specimen distance and size. a. Pairwise correlation function demonstrates evidence for pairwise associations. Values of $\hat{G}_{obs}(r) > G_{Pois}(r)$ indicate a clustered spatial distribution while $\hat{G}_{obs}(r) \approx G_{Pois}(r)$ 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.)

5.2. 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* appear to have been 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, directional 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, thus supporting our third hypothesis. Therefore, 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.

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 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 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) could imply a budding reproductive method. However, as a counter to this, the pairs are rarely observed touching and the size of individuals constituting 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 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* we observed 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 bilaterial 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.

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Chapter 4

Morphological plasticity in the Ediacaran fossil organism *Parvancorina* suggests a single species

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Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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4.1 Abstract

Fossils of the Ediacara Biota represent the earliest evidence of complex, multicellular life on Earth, and thus provide unique insights into the diversification of ancient animal life and its evolutionary strategies. The Ediacaran fossil *Parvancorina* is a small and enigmatic, shield-shaped organism found within Ediacaran deposits of both the Flinders Ranges of South Australia and the White Sea of Russia. Two described species of *Parvancorina* — *Parvancorina minchami* and *Parvancorina sagitta* — present gross shape disparity: *P. minchami* is laterally wider while *P. sagitta* is comparatively narrow. However, *Parvancorina* specimens commonly have highly variable shapes outside of these general patterns. Here, we demonstrate a gradient in shape exhibited between the morphotypes of the two prescribed species, using geometric morphometrics. We assessed shape variation among 213 individuals of *Parvancorina* to show that species diagnoses have not accounted for the shape variability characterising the two morphotypes. Instead, we suggest that the observed variability is attributed to morphological variation within a single species. Our findings emphasise that traditional methods of length and width alone, are insufficient to assign species identity among Ediacaran fossils.

4.2 Introduction

The fossils of the Ediacara biota from the Flinders Ranges of South Australia and White Sea of Russia (c. 555 Ma; Martin *et al.* 2000) record a glimpse into some of Earths earliest macroscopic marine benthic organisms (Droser *et al*. 2017). These Precambrian deposits present strong evidence for the early existence of complex metazoans (Glaessner 1958; Gold *et al.* 2015; Bobrovskiy *et al*. 2018) and possibly molluscs (Fedonkin & Waggoner 1997). Study of these organisms continues to document the drivers of early metazoan evolution.

One such iconic, yet understudied Ediacaran organism is the small, shield-shaped and epibenthic organism *Parvancorina* (Glaessner 1958; Glaessner 1980; Darroch *et al.* 2017; Paterson *et al.* 2017). *Parvancorina* is preserved as negative hyporelief in the base of siliciclastic beds in the Flinders Ranges and the White Sea (Glaessner 1958; Ivantsov *et al.* 2004; Gehling & Droser 2013). Two *Parvancorina* species have been described using length and width measurements: *P. minchami* (Glaessner 1958) varies considerably in shape from 'almost circular to transversely or longitudinally elliptical' (Glaessner 1958, pp. 86) and is found in both localities, while *P. sagitta* (Ivantsov *et al.* 2004) is axially oblong and found only in the White Sea in Russia (Naimark & Ivantsov 2009) (Fig. 1). Studies of hundreds of *P. minchami* from the Flinders Ranges have revealed great shape variability (Glaessner 1958; Ivantsov *et al.* 2004; Naimark & Ivantsov 2009); however, this shape variation has never been statistically quantified. Gradation between the two morphotypes (see middle specimens in Fig. 1) is noted, questioning the use of length and width alone to define a species.

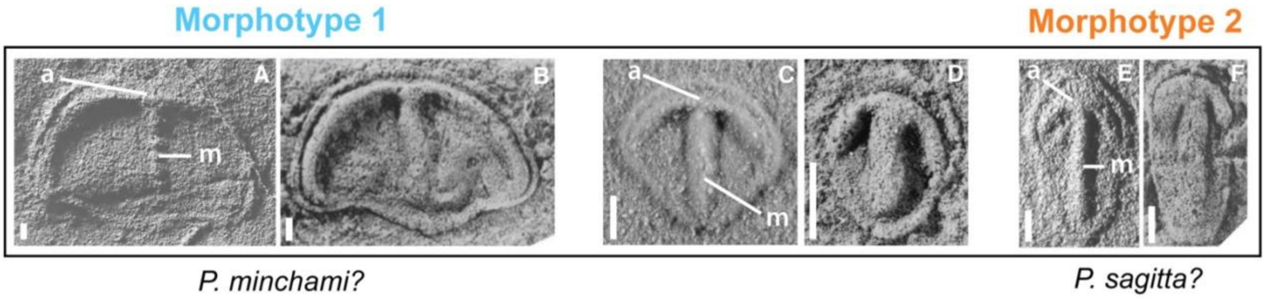

Figure 1. The two-described species of *Parvancorina* demonstrate extremes in shape variation. Specimens so far described have been assigned either to *P. minchami* ('Morphotype 1') or *P. sagitta* ('Morphotype 2'). The middle two specimens show an intermediate *Parvancorina* morphology. The anchor-shaped ridge has two components: the anterolateral ridge (a), and the medial ridge (m). Scale bars = 2 mm. Specimens A (Field specimen 1TF plinth), C (SAM P40433) and E (SAM NP27) are from Flinders Ranges deposits. Specimens B (PIN no. 399/6290), D (PIN no. 3993/6298) and F (PIN no. 4853/92) are from White Sea deposits (modified from Naimark & Ivantsov 2009).

Glaessner (1980) studied 60 specimens of *Parvancorina minchami* from South Australia and observed extensive morphological variation. However, he did not assess this quantitatively, and considered this variation as random post-mortem distortion. The same study interpreted *Parvancorina* as a proto-arthropod due to ridges (possible appendages) in the largest specimens. Further studies compared *Parvancorina* to Cambrian trilobitomorphs (e.g., *Primicaris*; Zhang *et al.* 2003, and *Skania*; Gehling 1991, Lin *et al.* 2006); however, more recent research has rejected this classification (Legg 2015; Darroch *et al.* 2017; Paterson *et al.* 2017). Another interpretation indirectly associates *Parvancorina* with the Mollusca (Ivantsov *et al.* 2004).

A semilandmark and landmark-based geometric morphometric analysis of 93 *Parvancorina minchami* from '*Parvancorina* Bed' ('Parv Bed') excavated at Nilpena fossil site (Flinders Ranges) (Fig. 2) documented high shape variation (Paterson *et al.* 2017). However, their study only examined the anchor-shaped ridge of *P. minchami* (Fig. 1). Since Paterson et al. (2017), an additional third of the Parv Bed has been excavated, increasing the bed area from ca. 7 m² to ca. 10 m². The autecology of *Parvancorina* was recently explored to show evidence of complex behaviour, such as: facultative mobility (Darroch *et al.* 2017), alignment with benthic currents (Coutts *et al.* 2016; Darroch *et al.* 2017; Paterson *et al.* 2017) and spatial aggregation (Coutts *et al*. 2018). Further, suspension feeding has been proposed as a potential feeding method (Darroch *et al.* 2017; Paterson *et al.* 2017).

Here, we expand on Paterson *et al*. (2017) and present new data concerning *Parvancorina* shape variability using landmark-based geometric morphometrics (*geomorph*) on 213 specimens. These specimens are from various locations within the Flinders Ranges of South Australia and include ten published specimens from the White Sea in Russia (Naimark & Ivantsov 2009). In this paper, we consider two main questions as a way of testing the cause of shape variability among *Parvancorina*: (1) Based on shape, is there evidence for the presence of two different species? (2) What are the sources (i.e., biotic or abiotic) of the observed shape variability?

4.3 Geological setting

The topographically complex geosyncline constructing the Flinders Ranges of South Australia preserves some of the earliest macroscopic animal communities on Earth. Ediacaran fossils are confined to the Ediacara Member unit within sedimentary deposits that fill a trough incised into the Chace Quartzite Member and Bonney Sandstone (Fig. 2) (Gehling, 2000). The Ediacara Member consists of a feldspathic quartz sandstone dominated sequence interpreted to have been deposited across a range of shallow marine and deltaic settings (Gehing and Droser, 2013, Droser et al., 2017). Fossils are typically found on the

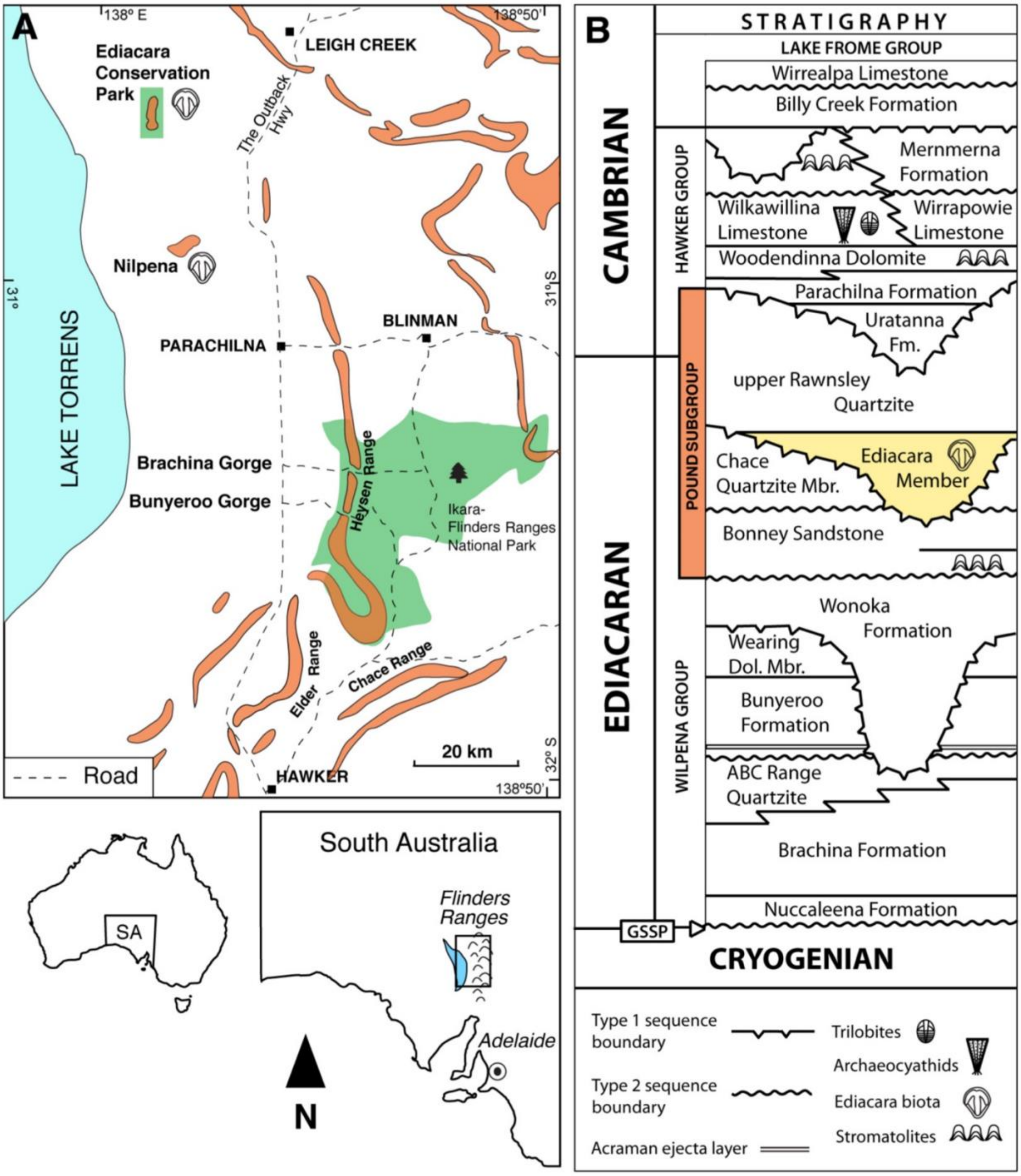

Figure 2. Pound Subgroup outcrops throughout the Flinders Ranges containing the fossiliferous Ediacara Member. **A,** location map illustrating the Pound Subgroup (orange) which contains the fossiliferous unit. The *Parvancorina* Bed is found within the National Heritage Listed fossil site of Nilpena, marked by the fossil icon. *In situ* fossil beds MM3 and 1TF are also found in Nilpena. **B,** stratigraphic section of the Flinders Ranges, showing the relative position of the fossiliferous Ediacara Member unit. Figures modified from Coutts *et al.* (2016) and Gehling & Droser (2012).

bases of pinkish- to reddish-grey fine to medium-coarse grained sandstones where

Ediacaran communities were buried beneath sequential sand depositional events possibly mediated by waning storm events (Gehling & Droser 2012). Less commonly, transported organisms were preserved in mass-flow sandstone facies in deeper, offshore settings (Gehling and Droser, 2013).

Parvancorina specimens are found *in situ* in most sedimentary facies (Gehling & Droser 2013). At the Nilpena fossil site a large assemblage of *in situ Parvancorina* are found on 'Parv Bed' (*n* = 119), where 97 specimens are preserved on a large contiguous 9.3 m² bed, and 22 specimens on non-contiguous float blocks of the same bed. Parv Bed is a fine- to medium-grained sandstone bed ranging between 12—16 cm thick (Paterson *et al.* 2017). Parv Bed belongs to the Planar-Laminated and Rip-Up Sandstone (PLRUS) Facies (Gehling & Droser 2013; Tarhan *et al*. 2017; Droser *et al*. 2017). The PLRUS Facies consists of laterally continuous, planar-laminated, fine-grained sandstone beds with erosive bases characterized, in places, by crisply preserved tool marks. Fossils of this facies occur as hyporelief external and internal molds (Droser *et al*. 2017). The PLRUS Facies is interpreted to represent sub-wavebase upper canyon fill, deposited under unidirectional flow (Tarhan *et al*. 2017)

The community preserved in this bed contains diverse Ediacaran fossil genera including: *Parvancorina*, *Dickinsonia*, *Eoandromeda*, *Funisia*, *Coronacollina*, *Ovatoscutum* and *Albumares*, as well as taxonomically unidentifiable fronds and several other undescribed forms and abundant textured organic surfaces (TOS) (Gehling & Droser 2009). Many scourmarks covered by textured organic surfaces demonstrate the scouring of the benthic substrate at high speeds prior to re-occupation by the preserved Ediacaran community (Paterson *et al.* 2017). The orientation of felled fronds preserved in the bed (Supplementary Fig. 1) provides the final burial current direction (Paterson *et al.* 2017).

4.4 Materials and methods

4.4.1 Digitisation and shape analysis

Geometric morphometrics is a powerful tool for assessing shape variation in a population. We applied the *geomorph* computer suite (Adams *et al.* 2016) to analyse shape variation in 213 photographed *Parvancorina* specimens. Latex casts of individual specimens from Parv Bed were made in the field. Specimens from other localities were cast with either latex or two-part dental putty, with the exception of a few specimens that were already cast with a different casting medium. We photographed these using a Canon 50D camera with a Canon MP-E 65 65 mm macro lens, and photographed all other specimens with an Olympus Stylus TG-4 Tough Camera on microscope setting.

All images were used to construct the geometric morphometric dataset and landmark data. The computer program *Thin Plate Spline* (tps) suite (Rohlf 2004) was used to digitise the landmarks. All photographed specimens were imported into the computer program tpsUtil (v. 1.65) to create a tps file, after which the image files were imported into tpsDig1 (v. 1.4) and a scale was assigned to each specimen. Body length/width dimensions and length/width dimensions of the anterolateral and medial components of the anchor-shaped ridge were taken. The anchor-shaped ridge area and body area was digitised using the ‘curves’ tool in tpsDig1. Ten fixed landmarks were assigned to anatomically homologous points in the fossils and 36 semi-landmarks were placed along the curved outlines of the body and anchor-shaped ridge (Fig. 3).

The data were imported into R (R Core Team 2015) and analysed with the package *geomorph*. A Generalised procrustes Analysis (GPA) and a principal component analysis were used to analyse landmark data. The superimposed data were multidimentionally analysed with principal components analysis to visualise the shape variation. The *Csize* function was used to assess *Parvancorina* specimen size (Adams *et al.* 2016).

Parvancorina height was determined by measuring the height of the intersection between the anterolateral ridge and medial ridge (see Fig. 1). Useful specimens (n=67) were cast in two-part putty and axially dissected to the left of the midline. The right side was photographed to assess the cross-section. The photographs were digitised using the same methods outlined above, and height measured using tspDig.

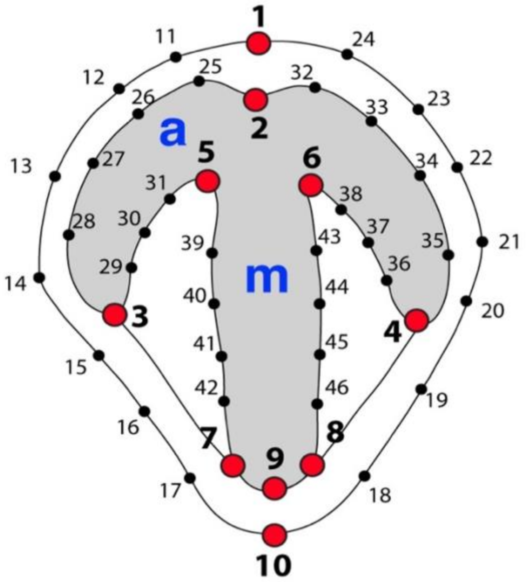

Figure 3. Generalised illustration of *Parvancorina* displaying the position of the landmarks we used in this study. Red dots are fixed landmarks, black dots are semi-landmarks. The grey-filled anchor-shaped ridge consists of two measurable components: a = anterolateral ridge; m = medial ridge.

4.4.2 Spatial and orientation analyses

Six years after the initial excavation and re-assembly of the Parv Bed at the National Heritage Listed fossil site, an additional third of the final Parv Bed was excavated, inverted, reassembled, cleaned and added to the original reassembled bed sole sample, in line with the outcropping bed. After removal of silt from the excavated bed, a fabric-backed rubber latex cast (of 12 layers) was made of the entire surface area (9.3 m^2). Exact positions of *Parvancorina* were obtained by overlaying a plastic sheet with a 20 × 20 cm grid, onto which, coordinates were recorded.

Dominant bottom-water current direction was derived using the orientation of scourmarks and felled fronds (see *Geological setting* for more details), and these were recorded as a measure of their angular deviation from the grid lines. To assess any trends in the spatial distribution of *Parvancorina* on the Parv Bed, we did a nearest-neighbour cluster analysis of the specimens using the function *Gest* in the R package Spatstat (Baddeley *et al.* 2015). We used ggplot2 (Wickham 2009) to produce rose diagrams and size-frequency histograms. We used a Kolmogorov-Smirnov test implemented through the function *ks.test* in the R package stats to assess discrepancies within the *Parvancorina* population structure on Parv Bed.

4.5 Previous systematic descriptions of *Parvancorina* species

Genus ***Parvancorina*** Glaessner, 1958

The genus *Parvancorina* was first described by Glaessner (1958) based on several figured specimens discovered by amateur geologists Hans Mincham and Ben Flounders in 1957, from fossiliferous beds of the "Pound Sandstone" in what is now Ediacara Conservation Park (Glaessner, 1958) (see Figure 2A). *Parvancorina sagitta* was described by Ivantsov *et al*. (2004) from Ediacaran-aged sedimentary strata on the Onega Peninsula of the White Sea coast in the Arkhangelsk region, Russia. The description of *P. sagitta* was based on the different length/width ratio of its 3 type specimens with *P. minchami* (Ivantsov *et al.* 2004). Further, Ivantsov *et al*. (2004) noted particular anatomical differences in the dorsal anatomy between *P. minchami* and *P. sagitta*. These features included the latter having a more elongate body, wider peripheral rim, wider medial ridge and narrower anterolateral ridge (Ivantsov *et al.* 2004). Inversely, *P. minchami* has a wider anterolateral ridge and less elongated body (Glaessner 1958).

The original diagnoses of *P. minchami* and *P. sagitta* were as follows:

Parvancorina minchami Glaessner, 1958

(Fig. 1A–D)

> 'A small shield-like body, oval in outline, slightly wider in front(?) where its margin is curved in a low arc, and gently tapering to the rounded end. Margins slightly raised so as to form a rim which is little more prominent at the wider end. The centre is occupied by a prominent, smooth, anchor- or T-shaped ridge which is unsegmented and undivided. It is separated by a distinct furrow from the anterior(?) rim, while its longitudinal bar rises above a flat surface between the covering posterior(?) contours. No appendages are known.' (Glaessner 1958, p. 187).

Parvancorina sagitta Ivantsov et al., 2004

(Fig. 1E, F)

> ‘The body is elongated oval with a wider, tentatively anterior end. A narrow band slightly widened anteriorly and posteriorly extends along the margin of the body. The central part of the body is evenly convex in small specimens, while in the larger specimens, the central area is occupied by an anchor-like ridge. The transverse beam of this structure is arched, the distance between its ends is about half of the whole length of the structure. The longitudinal beam is straight and relatively wide.’ (Ivantsov *et al.* 2004, p. 7).

4.6 Results

4.6.1 Two ‘morphotypes’

The Principal Component (PC) plot of Parv Bed (*n* = 71) shows two distinct groups (Fig. 4). PC1 documents variation along the longitudinal axis (55.6% of variation) and separates laterally wider specimens (blue circles) from laterally narrower specimens (orange crosses), PC2 mainly explains size morphology (9.4% of variation). The two groups defined along PC1 show two shape extremes (Figs. 1 and 4). Morphotype 1 specimens in most negative PC1 space have a length/width ratio of approximately 1:2, are more equidimensional and closer

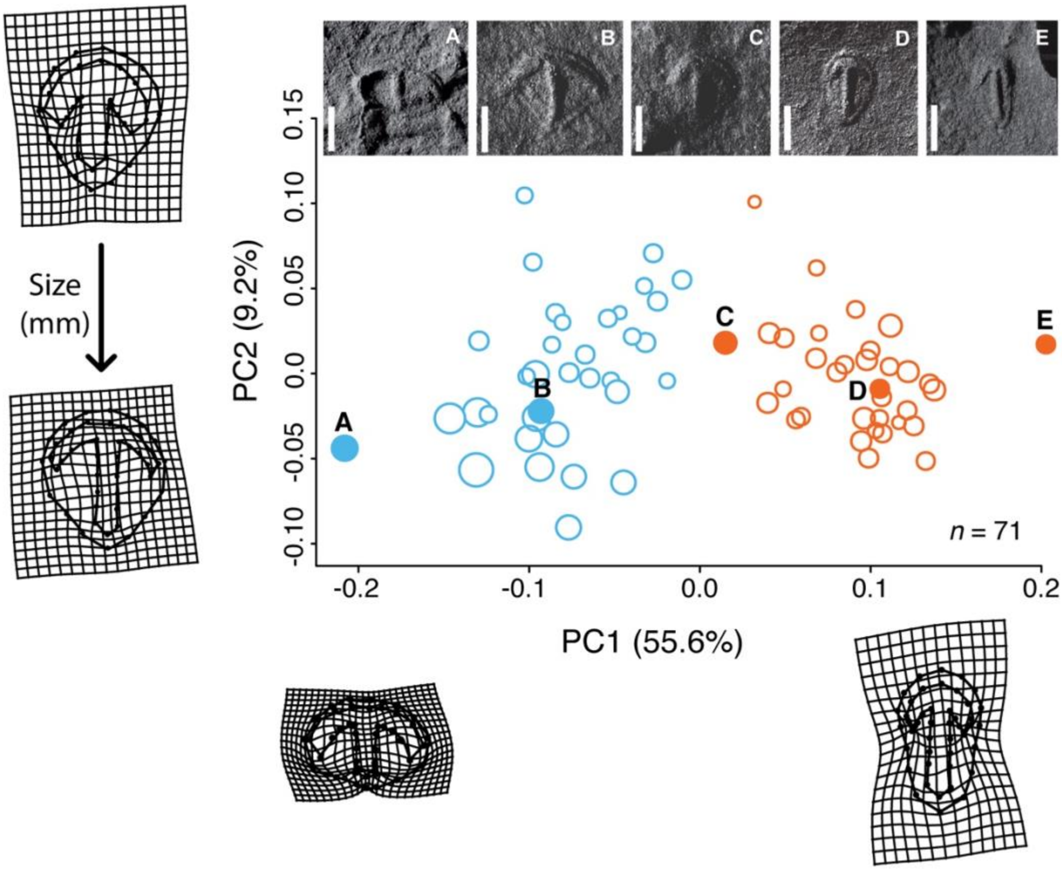

Figure 4. Principal components plot of the Parv Bed specimens showing two groups and extreme shape variability. Principal component 1 (PC1) explains 55.6 % of the variance in the data, and principal component 2 (PC2) explains 9.2 % of the variance. Morphotype 1 (left blue circles) range between lateral expansion (left warpgrid, specimen A) and equal length and width. Morphotype 2 (right orange circles) varies between roughly equal in length and width (specimen C) to elongated (right warpgrid and specimen E). PC2 shows the anchor-shape change relative to body size. Centroid size (a measure of size used in geometric morphometrics) in principal-component space is demonstrated by circle size in plot. Size increases overall with a decrease in the ratio of the anchor area/body area. The ridge covers a larger surface area in smaller specimens, while larger specimens have proportionately less ridge surface (see top and bottom warpgrids). Photographs are of specimens from the Parv Bed. Specimens A–E: SAM NP25, SAM NP23, SAM NP22, SAM NP24, SAM NP26. Scale bars = 0.5 mm.

to PC1=0 (Fig. 4). Morphotype 2 has a similar variability where specimens are approximately equidimensional at PC1=0 and have a length/width ratio of approximately 2:1 in positive PC1 space (Fig. 4).

4.6.2 *Parvancorina* demonstrate ontogenetic development

Both morphologies show similar shape variability along PC2. PC2 shows that the anchor-shaped ridge is dominant in smaller specimens and less dominant in larger specimens (see size gradient of circles as well as PC2 warpgrids in Fig. 4). This observation is reconfirmed when plotting anchor-shaped ridge area (mm^2) against body area (mm^2) in the larger sample ($n = 213$) (Supplementary Fig. 2A and B), and shows a strong correlation between the two variables (log-transformed plot: $p = 2.2 \times 10^{-16}$, $R^2 = 0.98$). Smaller specimens have a proportionally larger ridge, and the dominance of the ridge decreases with increased specimen size. This is indicative of an ontogenetic trend rather than morphological trend. The specimens featured in Figure 4 were used as they were all of a similar size and convey the gross shape variability observed among specimens. Importantly, the warpgrids demonstrate that the bilaterally symmetrical shape of *Parvancorina* is maintained in PC space (Fig. 4).

The relationship between the medial ridge/anterolateral ridge length (mm) and whole-body length/width (mm) ratio was examined for both individual morphotypes and as a complete population (Fig. 5A). When considering both morphotypes, a very strong correlation was found ($p < 0.0001$ and $R^2 = 0.70$; Fig. 5A), contrary to when the morphotypes were considered independently. Importantly, an inverse relationship between the two proportions demonstrated a shape change from laterally wide to laterally narrow anterolateral ridge lengths and medial ridge lengths (Fig. 5A), suggesting that an increase in the length of one shortens the other.

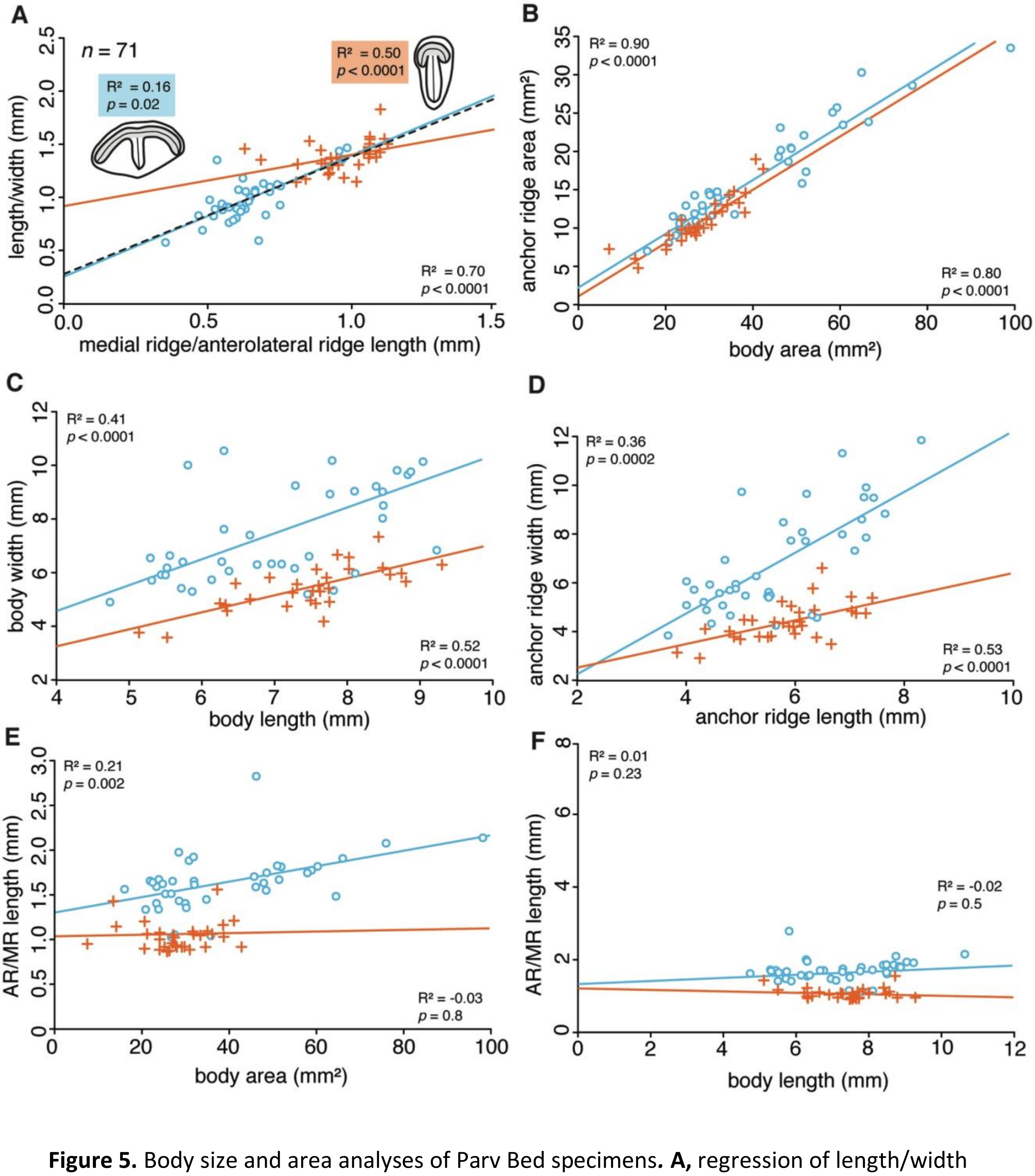

Figure 5. Body size and area analyses of Parv Bed specimens**. A,** regression of length/width (mm) against medial ridge/anterolateral ridge length (mm) in Morphotype 1 (blue circles) and Morphotype 2 (orange crosses) specimens, respectively. Morphotype data combined shows the strongest correlation (black dotted line, $p < 0.0001$ and $R^2 = 0.70$). As the medial ridge in *Parvancorina* lengthens, the anterolateral ridge shortens proportionally, and vice versa. **B,** anchor ridge area (mm²) against body area (mm²) was similar in both morphotypes and demonstrated a strong allometric correlation. **C,** body length against body width in both morphotypes demonstrated a weak but positive correlation.

Figure 5 continued. (Morphotype 1: $p < 0.0001$ and $R^2 = 0.41$; Morphotype 2: $p < 0.0001$ and $R^2 = 0.52$). **D**, anchor ridge length against anchor ridge width regression plot shows that the anchor ridge width in Morphotype 1 specimens increases with size at a greater rate than Morphotype 2 specimens. **E–F,** plots of anterolateral ridge/medial ridge length against both body area (E) and body length (F) demonstrate no evidence for allometry with size.

The relationship between anchor-shaped ridge area and total body area in both morphotypes were examined. The areas had a strong positive correlation ($R^2 > 0.80$, $p < 0.0001$) (Fig. 5B) and were highly constrained compared to overall length and width measurements of specimens ($R^2 < 0.53$, $p < 0.0001$) (Fig. 5C). We found that body and anchor ridge measurements were more constrained in Morphotype 2 than Morphotype 1 (Fig. 5C and D). No correlation between anterolateral ridge/medial ridge length was found with body area or length with size (Figs 5E and 5F).

4.6.3 Population structure

Parvancorina size-frequency distribution on Parv Bed is slightly left-skewed (Fig. 6A): specimen length ranges between 2.3 – 13.7 mm (median ± standard error = 7.8 ± 1.6 mm). As a null hypothesis, we treated Morphotype 1 and Morphotype 2 as distinct populations and by extension, different species. Interestingly, within each morphotype group, specimens showed variability in shape and size frequency, with the most specimens within each group peaking in the middle of each group and then fewer specimens gradually towards an equidimensional shape toward PC1 = 0 (Fig. 6B). We failed to reject the null hypothesis of a difference in number of individuals between the two morphotypes (Komolgorov-Smirnov *p*

= 0.15) (Fig. 6C), suggesting that both morphotypes are from the same population, and that the existence of two species is unlikely.

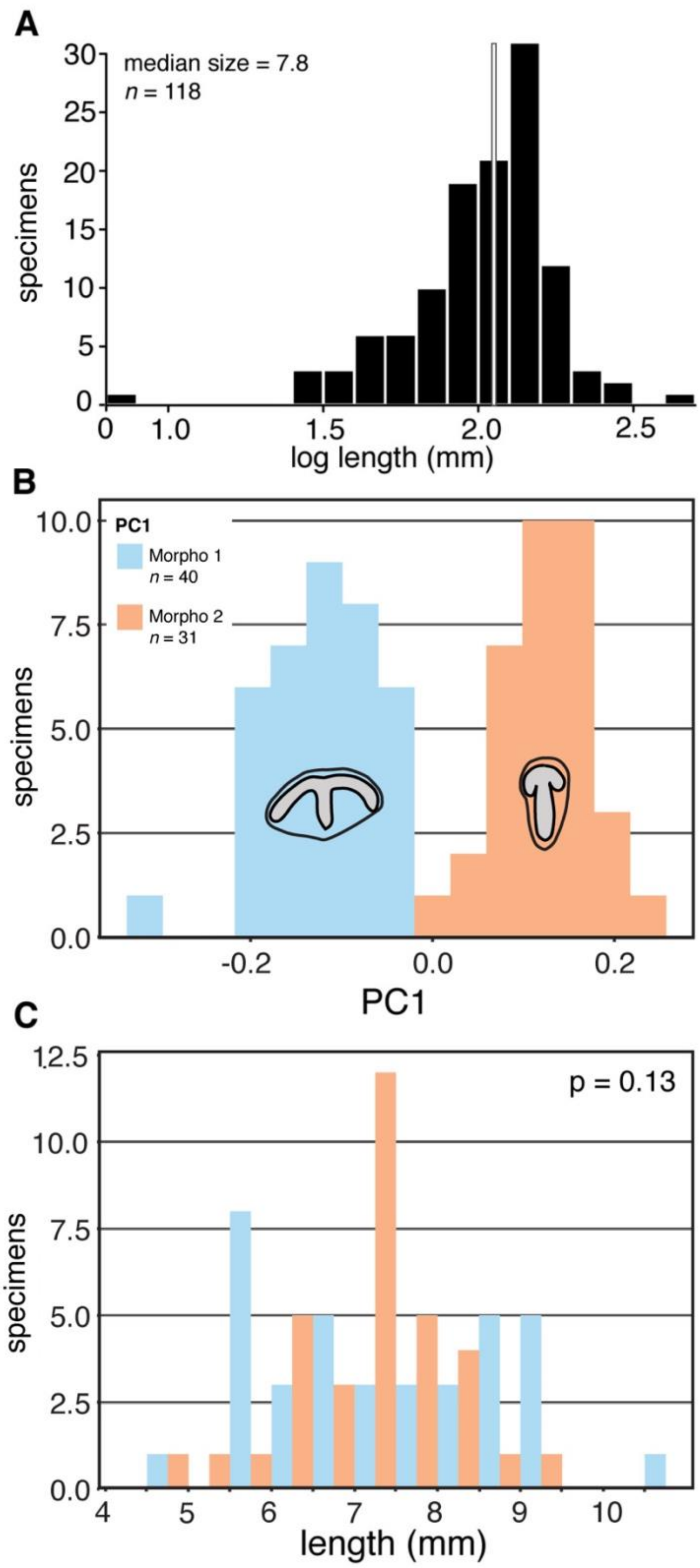

Figure 6. Histograms of specimens from Parv Bed**. A,** log$_{10}$-transformed length distribution of *Parvancorina* specimens from the Parv Bed and its non-contiguous float slabs. The white rectangle indicates median specimen length (mm). **B,** distribution of PC1 values showing the two Morphotypes. Morphotype 1 is highlighted in blue, while Morphotype 2 is highlighted in orange. **C,** length distribution of Morphotype 2 superimposed on Morphotype 1, showing similar population

4.6.4 Burial current

Ediacaran communities are preserved as impressions in the soles of sandstone beds. This preservational mode provides insight into the paleoecology and abiotic processes that preserved these fossils. Unidirectional scourmarks on Parv Bed have a mean orientation of 247° from north (south pointing to the origin of the bed in the hill side, Supplementary Fig. 1A) and indicate that strong benthic currents probably affected the seafloor before the *Parvancorina* community developed (Paterson *et al.* 2017). Frond impressions on Parv Bed support this hypothesis. These fronds were felled and fossilized parallel with the prevailing burial current direction of 245° from North (Supplementary Fig. 1B). Morphotype 1 had a strong principal orientation with the putative current direction where the widest end of the fossils are facing down-current (Fig. 7B). Morphotype 2 specimens were primarily orientated in two directions: perpendicular and parallel to the current.

Morphotype 2 also showed more scatter in its orientations than Morphotype 1. The shape of the specimens might have therefore been influenced by, or associated with, prevailing benthic currents (Darroch *et al*. 2013). Shape and orientation are likely related in

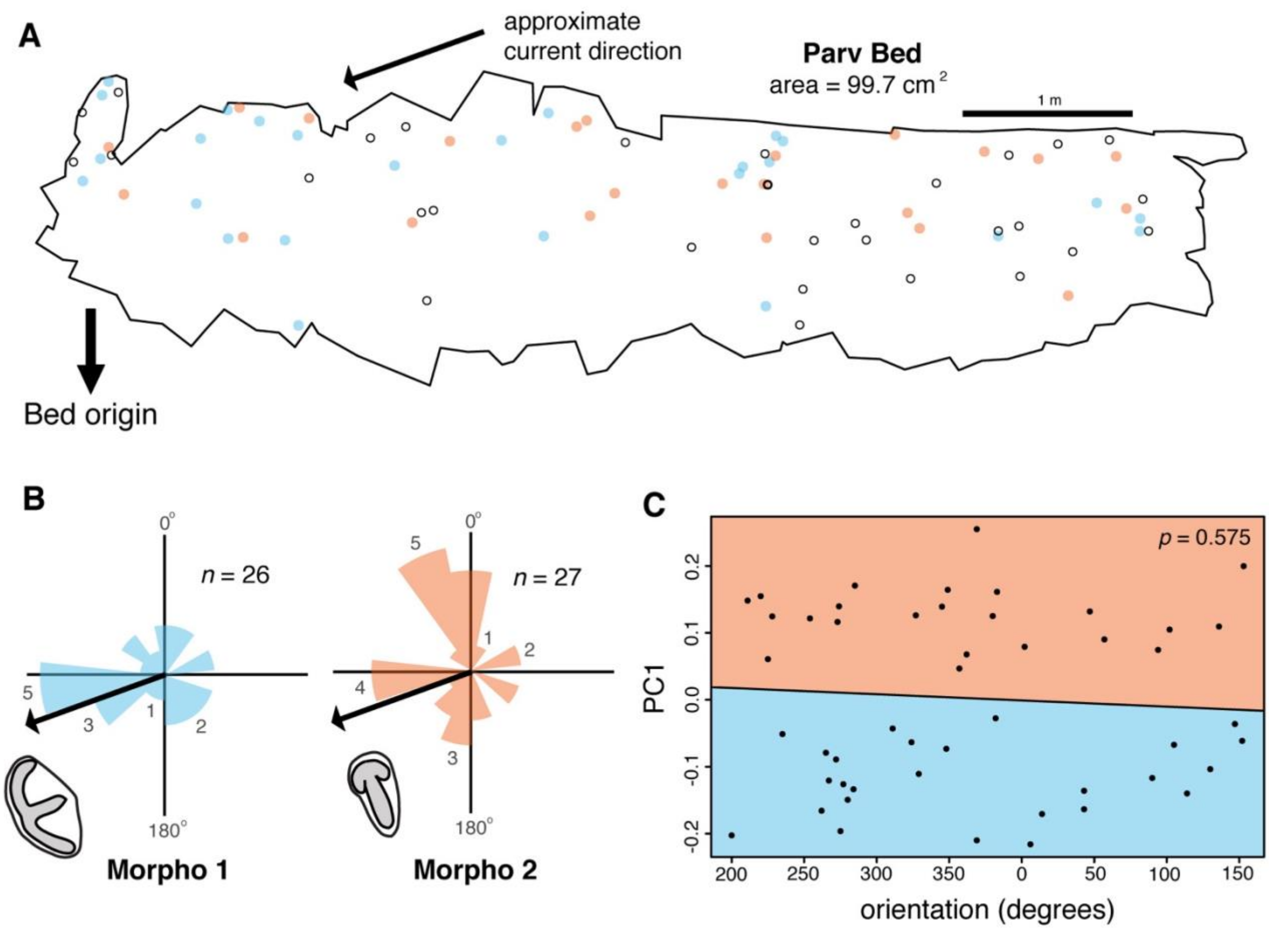

Figure 7. *Parvancorina* Morphotypes 1 and 2 exhibit different trends in orientation to benthic currents as determined by fronds and scourmarks in Parv Bed (see Supplementary Fig. 1). **A**, sketch of the Parv Bed showing the relative positions of *Parvancorina* on the surface (circles), including: Morphotype 1 (blue), Morphotype 2 (orange) and specimens that were not preserved well enough for shape analysis (white). **B,** rose diagrams indicating the main alignment of Morphotype 1 to the current direction (left), and the dual alignment of Morphotype 2 specimens with the current and perpendicular to the current (right). **C,** regression analysis of *Parvancorina* shape (PC1) against orientation angle. No gradient in shape based on orientation respective to the current direction is evident.

Morphotype 1 specimens, but the scatter and orientation of >7 Morphotype 2 specimens suggest that shape was influenced by other factors also (Fig. 7B). These results contradict Paterson *et al*. (2017) who found that *Parvancorina* was unidirectionally aligned with the putative burial current.

4.6.5 Comparison with other Australian specimens and with Russian material

Among the larger sample size (*n* = 213), the PCA revealed a gradient in shape between Morphotype 1 to Morphotype 2 along PC1, with no clear differentiation between morphotypes (Fig. 8A). The three described *P. sagitta* from the White Sea (Russia) fell into the principal component space of Morphotype 2 (Fig. 8A). However, two of the prescribed White Sea *P. minchami* (specimens D and E in Fig. 8A) also fell well within the parameters of Morphotype 2 with PC1 values > 0, placing them within the shape-space closest to *P. sagitta* specimens.

Consistent with the analysis of the *in situ* Parv Bed specimens (Fig. 4), a relationship between size and anchor-shape ridge is evident. When we plotted the calculated centroid

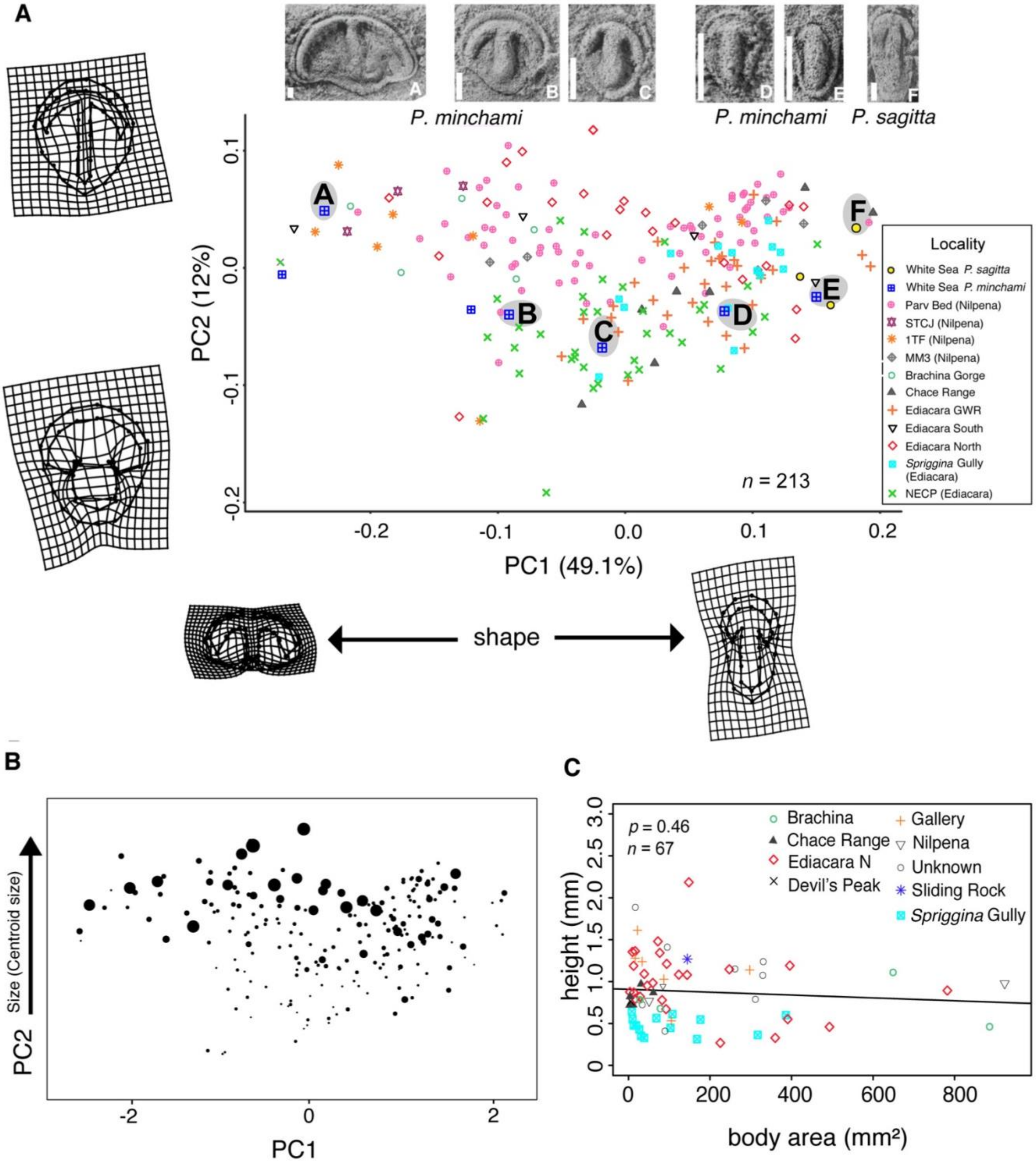

Figure 8. Specimens from multiple localities demonstrate a gradient in shape change. **A,** principal component plot of 203 *Parvancorina* specimens from the Flinders Ranges of South Australia and 10 specimens from the White Sea, Russia (Naimark & Ivantsov 2009). Shape changes from wide to narrow along PC1, while PC2 indicates variation in anchor-shaped ridge with size such that the ratio of ridge area/body area decreases with growth. Two of the prescribed White Sea *P. minchami* fall within the parameters of Morphotype 2 (specimens D and E).

Figure 8 continued. B, centroid size in principal-component space. Size increases overall with a decrease in the ratio of the anchor area/body area. **C,** regression of *Parvancorina* height (mm) against body area (mm^2) reveals that smaller specimens have greater relief for their size compared to larger specimens. We chose specimens randomly, originating from more than seven different localities in the Flinders Ranges. Specimens A (PIN no. 3993/6290), B (PIN no. 3993/6311), C (PIN no. 3993/6298), D (PIN no. 3993/6214), E (PIN no. 3993/6156) and F (PIN no. 4853/92) from White Sea deposits (modified from Naimark & Ivantsov 2009). Scale bars = 2 mm.

size (a measure of organism size) in the principal-component space, we found that anchor area relative to body area decreased with size (Fig. 8B).

4.6.6 *Parvancorina* was a low-lying organism

Among a random sample of *Parvancorina* specimens (*n* = 67), height analyses showed that variation in fossil relief occurred as a combined result of taphonomy and biological size (Fig. 8C). In the first instance, there appears to be a connection between locality and fossil height. For example, fossils from Chace Range in the southern Flinders Ranges consistently tend to have high relief (Gehling 1999) (Fig. 8C). Additionally, smaller *Parvancorina* specimens demonstrate proportionally higher relief than larger specimens (Fig. 8C). As body area increased with size, the ridge height remained similar or decreased (possibly an artefact of compaction of a larger organism). This suggests that as specimens grew larger, they maintained a low profile above the seafloor.

4.7 Discussion

Taphonomic bias can modify how morphological variation is interpreted in palaeontology. As such, taphonomy must be considered when assessing fossil material (Goldring 1995; Zhu *et al.* 2006). Extreme morphological variants are often assigned to a new species, but such an approach is flawed when considering *Parvancorina*. Evidence presented from Parv Bed and other localities suggest that ontogeny and morphological plasticity best explains the observed variation in *Parvancorina* shape.

We show that *Parvancorina* exhibited ontogenetic development, where, the ridge is more pronounced in smaller specimens compared to larger specimens (Naimark & Ivantsov 2009). The higher and thicker anchor-shaped ridge may have reduced the functional flexibility in smaller specimens, and increased the dorsal influence of benthic currents (Coutts *et al*. 2018). This explains why the smallest *Parvancorina* specimens are oriented parallel to benthic palaeo-currents (Coutts *et al*. 2018). Conversely, larger specimens had thinner anchor-shaped ridges and lower relief above the seafloor. Larger specimens therefore had less structural support and are occasionally preserved over-folded and deformed from burial (Fig. 9Biii), especially in the inter-ridge space (Fig. 9Biv) (Glaessner 1980; Paterson *et al.* 2017). A possible advantage of being thinner, and perhaps more flexible, as an individual aged could have increased dispersal ability, as individuals with more flexibility would have the potential to explore and exploit a wider range of habitats.

Parvancorina anchor-shaped morphology has been interpreted as either a feeding mechanism or used in reproduction (Naimark & Ivantsov 2009; Darroch *et al.* 2017; Paterson *et al.* 2017). Alignment of *Parvancorina* with benthic currents, observed both physically (Coutts *et al.* 2016; Paterson *et al.* 2017) and through modelling (Darroch *et al.* 2017) confirms the active orientation of *Parvancorina* with benthic currents (Darroch *et al.* 2017). Suspension feeding with features on the proximal side of the anterolateral ridge, could be a plausible explanation the orientations observed (Paterson *et al.* 2017). However, suspension feeding cannot explain the reduced anterolateral ridge length in Morphotype 2 specimens. Species of Morphotype 2 may have been orientated perpendicular to the current and slowed currents over the body with the medial ridge. However, the shortened anterolateral ridges of Morphotype 2 compared to Morphotype 1 does not support this

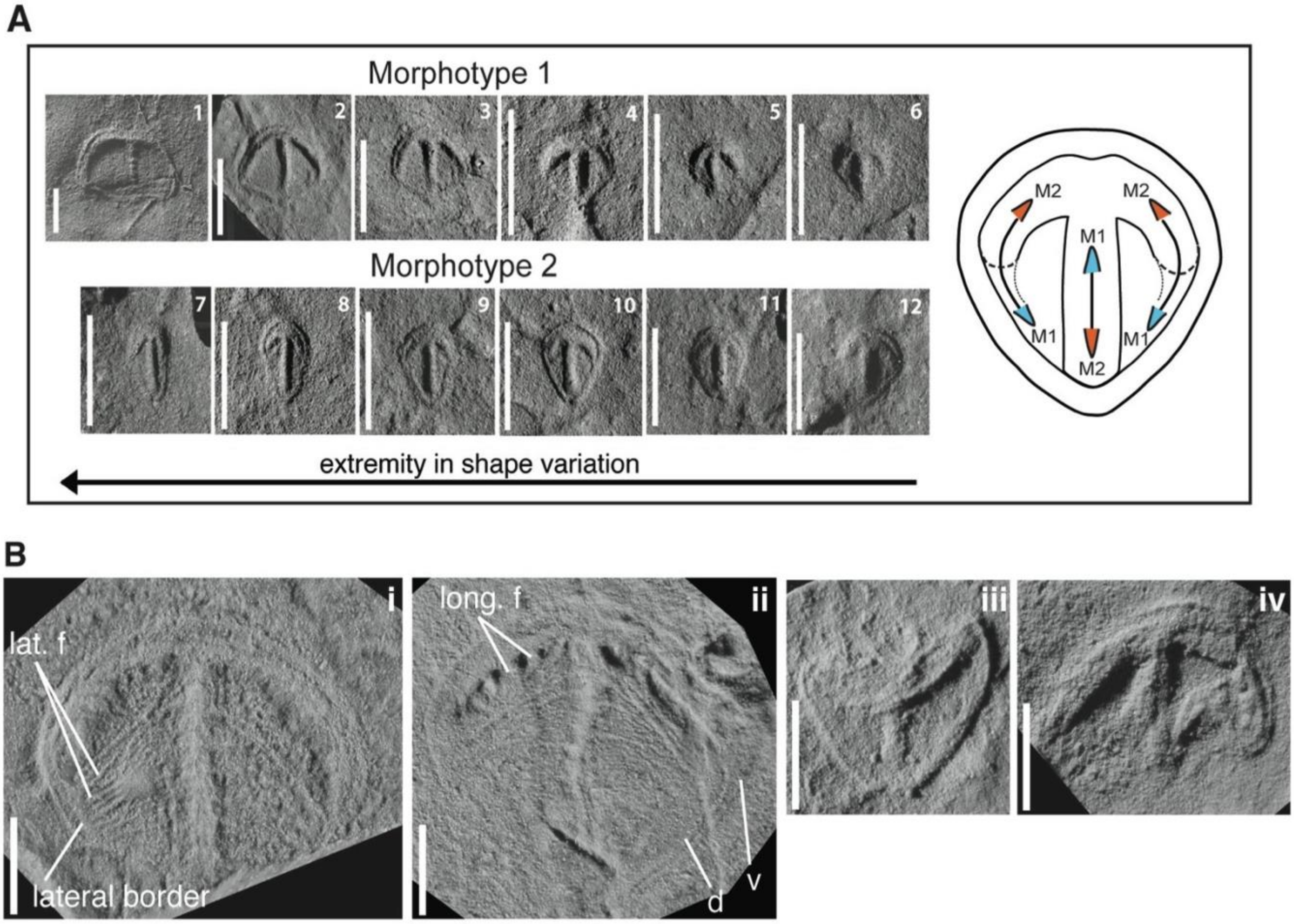

Figure 9. *Parvancorina* presents a gradient in shape. **A,** shape variability exhibited among Morphotype 1 and Morphotype 2 specimens. Generalized *Parvancorina* (right) showing a proposed path of shape change independent of body size: as the anterolateral ridge lengthens, the medial ridge shortens proportionally, and *vice versa*. Specimens 1–12: Field specimen 1TF plinth, NP35, NP34, NP32, NP30, NP29, NP26, NP27, NP33, NP31, NP28, NP22. **Bi–Bii,** some of the largest specimens of *Parvancorina* show details of possible internal lateral and longitudinal structures. lat. f = lateral filaments(?), long. f = longitudinal filaments(?), d = dorsal tissue, v = ventral tissue (SAM P2130021, SAM P2130020). **Biii–Biv,** over-folded and distorted examples of *Parvancorina* (SAM P14251, P40426). Scale bars = 10 mm.

interpretation. Nonetheless, the benefits of a narrower body or smaller dorsal area might have been associated with less drag in benthic currents (Darroch *et al.* 2017).

Apparent morphological plasticity exists within both morphotypes of *Parvancorina* from Parv Bed. Furthermore, the anchor-shaped ridge area and body area with size among all specimens retained a strong allometric relationship between these two body components, despite the variance in body length and width observed. The gradient in shape variability suggest an ability to modify body proportions (Fig. 9A). Shortening of the medial ridge and lengthening of the anterolateral ridge would result in the most extreme Morphotype 1 individuals. Conversely, the lengthening of the medial ridge and shortening of the anterolateral ridge would result in Morphotype 2.

Regularly spaced longitudinal (Fig. 9Bi) and lateral filaments (Fig. 9Bii) are present in larger *Parvancorina* specimens (Glaessner 1980; Paterson *et al.* 2017). These may reflect internal structures imprinted through soft or thin overlying tissue. Wrinkles from compaction are unlikely as filaments consistently occur perpendicular to each other, and therefore must have had some structural integrity. Longitudinal filaments are widest (~ 1 mm in diameter) in proximal regions and have been suggested as potential suspension-feeding structures (Paterson *et al.* 2017). The longitudinal and lateral conformations of the structures are comparable to the two main body shapes of *Parvancorina*. Therefore, these structures may have allowed longitudinal and lateral contraction and expansion. Detailed analyses of these structures are needed to strengthen such an interpretation.

The tri-lobed body plan of *Parvancorina* coupled with the presence of lateral filaments, has led to comparisons with early Cambrian Trilobitomorphs (Glaessner 1980; Zhang *et al.* 2003; Lin *et al.* 2006). Yet, the variability in preservation and lack of evidence for distinct hard-parts in the dorsal morphology of *Parvancorina* implicates a soft-bodied interpretation. Furthermore, the ontogenetic trend associated with increased flexibility with age is distinct from the systematic trends of ontogenetic axial patterning in trunk (or medial) segmentation, common among Trilobites (Hughes 2007).

The morphological plasticity exhibited by *Parvancorina* could be analogous to that seen in soft-bodied invertebrates such as molluscs. For instance, each tentacle of a cephalopod encloses a muscular-like structure called a muscular hydrostat. Muscular hydrostats maintain constant volume as they proportionally elongate whilst becoming narrower and shorten while widening to provide extreme movement and shape variability (Kier & Smith 1985). Muscular hydrostats are present as specialized organs in vertebrates also (such as the tongue in humans, and the trunk in the elephant), and allow for complex and controlled, fluid movement (Kier & Smith 1985). Additionally, hydrostatic skeletons (fluid-filled cavities) allow highly varied shape change in many invertebrates such as annelids, cnidarians, nematodes, and echinoderms.

The differences between morphotypes could suggest sexual dimorphism. Lateral expansion of the anterolateral ridge in Morphotype 1 specimens has been tentatively considered a reproductive feature (Naimark & Ivantsov 2009). The anterolateral ridge could have housed gametes as it is a major area of growth in Morphotype 1 and comparatively stunted in Morphotype 2. Sexual dimorphism could also explain the larger size of Morphotype 1 compared to Morphotype 2 (Downing *et al.* 1989). Both sexes of species in living and fossil epibenthic marine communities are found together, suggesting that aggregation can be a function of sexual reproduction (Heip 1975). This explanation compliments the intimate spatial associations observed between both morphotypes on the Parv Bed. *Parvancorina* can be numerous within populations (Coutts *et al*. 2018), and cases of intimate 'behaviour' are common (Fig. 10). We report among the first evidence of physical contact in any bilaterally symmetrical Ediacaran fossil suggesting that sexual reproduction, described among other fossils of the Ediacara biota (e.g. Droser and Gehling (2008) may also have been the case for *Parvancorina*.

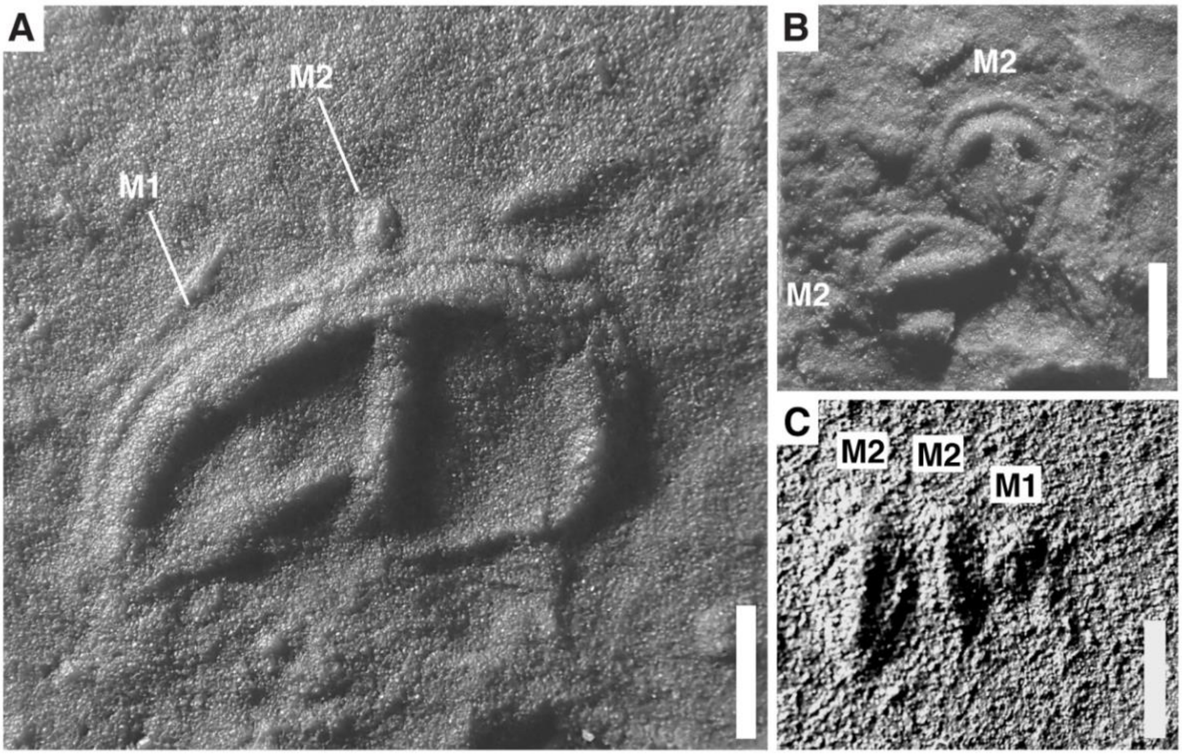

Figure 10. Morphotype 1 and 2 specimens show intimate spatial associations. **A,** large Morphotype 1 (M1) specimen (below) close to a juvenile Morphotype 2 (M2) specimen (M1: SAM P56774; M2: SAM P56775). **B,** two M2 specimens of analogous shape and size perpendicular to each other and touching distally (Top specimen: SAM P56776; Bottom specimen: SAM P56777). **C,** a trio of touching *Parvancorina* showing a gradient in shape (Left to right: SAM P57218; SAM P57219; SAM P57220). The specimens appear to be laterally touching approximately at the distal anterolateral ridge. Scale bars = 5 mm.

Computer modelling of *Parvancorina* hydrodynamics show that the widest specimens had the least drag when oriented perpendicular to a current (Darroch *et al.*

2017). Interestingly, the widest specimens on Parv Bed (Morphotype 1) were aligned parallel with burial current, and with their widest end facing down-current (see Fig. 7A). This indicates a connection between Morphotype 1 and the benthic current. Narrow specimens (or Morphotype 2) were less affected by the current compared to wider specimens (Darroch *et al.* 2017).

This is consistent with Morphotype 2 specimens being oriented both parallel and perpendicular to the current. The lack of relationship between orientation and shape suggests that the burial current did not affect all individuals equally. This could be caused by natural undulations in the seafloor creating heterogeneous patterns of flow over the organisms, or differences in original relief between the different individuals. The largely symmetrical and controlled shape configurations exhibited by *Parvancorina* suggests that shape was not entirely a result of current forces, but individuals also maintained some control over their body proportions during the burial event.

Naimark & Ivantsov (2009) suggested that Flinders Ranges *Parvancorina minchami* and White Sea *P. minchami* possibly represented different subspecies based on slight allometric deviations of length and width. We argue that this was a function of taphonomy and sampling bias. We observed variation in fossil preservation across localities and within beds in the Flinders Ranges (Fig. 8A). This variation was most likely caused by a variety of factors, including: variation in grain size, ocean geochemistry, depth, natural undulations in the seafloor, microbial-mat composition, community structure and population density.

The abiotic environment plays a key role in the evolution and morphological adaptations of living organisms (Goldring 1995; Zhu *et al.* 2006; Benton 2009). Similarly, the disturbance events of benthic sedimentation flows affected the persistence and composition of Ediacaran communities, and influenced community compositions (Wilby *et al.* 2015). Similar disturbance events conceivably drove the adaptation of mobility among the first animals, allowing them to recolonize and settle elsewhere (Droser *et al.* 2017). Sediment flow and forceful benthic currents may therefore have driven the evolution of *Parvancorina.*

4.8 Conclusion

Fossils of *Parvancorina* from both Flinders Ranges deposits in South Australia and White Sea deposits in Russia demonstrate a large amount of morphological variability. We have shown here that relying on using length and width alone is inappropriate for assigning classifications to such morphologically variable organisms, and that in the case of this genus, there appears to be a morphological continuum between the two 'species' described to date —: *P. minchami* and *P. sagitta*. Therefore, we conclude that there is insufficient evidence to claim the presence of two species within the genus, and suggest instead, only a single species of *Parvancorina* is evident: *Parvancorina minchami*.

The limited amount of material recovered for some Ediacaran organisms often leaves gaps in the morphological spectrum, making species identification difficult. We confirm that landmark-based morphometrics is an effective and informative way to assess shape among possible synonymous Ediacaran 'species', and suggest that this approach be adopted in the future. There appears to be a relationship between *Parvancorina* morphology and the surrounding environment — particularly with benthic palaeo-currents. Benthic environmental conditions were likely important in the evolution and diversification of the earliest animals, and should therefore be considered when assessing and interpreting the morphologies of Ediacaran fossils such as *Parvancorina*.

4.9 Acknowledgements

We thank the University of Adelaide and the South Australian Museum for access to literature and fossil material and R and J Fargher for access to the site. We thank Emma Sherrat for her advice on the morphometric analysis – this was particularly useful, thank you. We particularly thank Dr. 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. We would like to make a special acknowledgement of Coralie Armstrong, who passed away last year. Coralie has volunteered thousands of hours to Ediacaran palaeontology at the South Australian Museum, and her invaluable contributions will not be forgotten.

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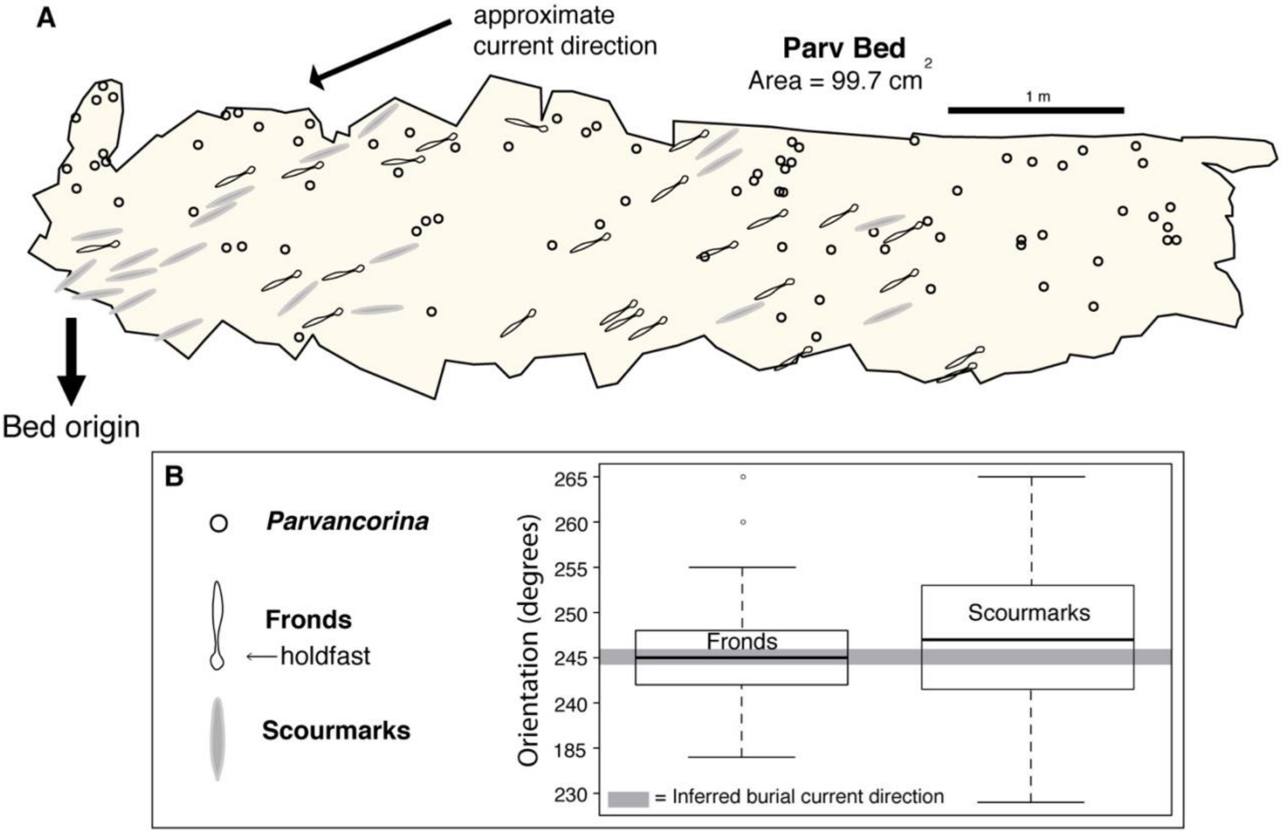
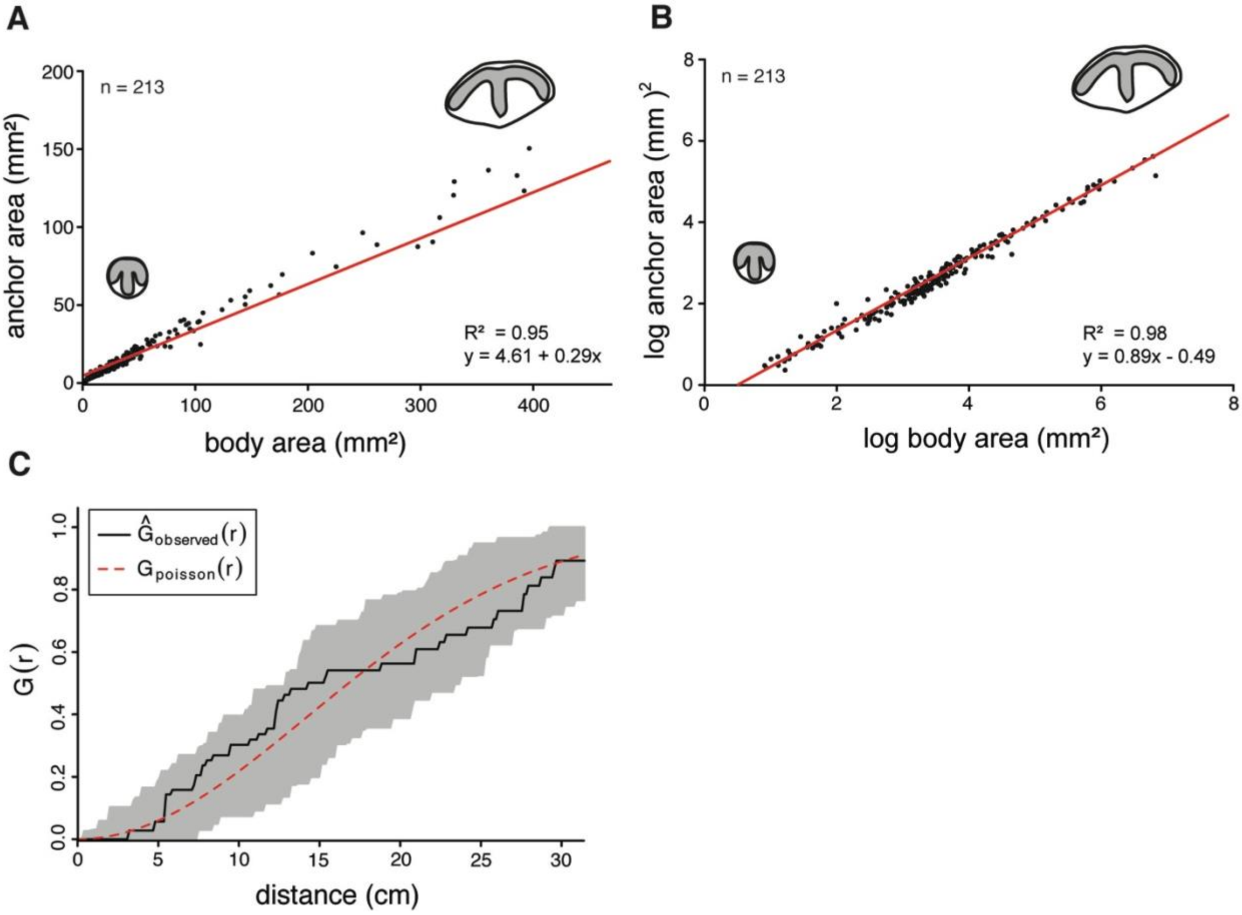
4.11 Supplementary Figures



Supplementary Figure 1. A, orientation histograms for the ‘fronds’ (*n* = 24) and scourmarks (*n* = 20) preserved on Parv Bed. Grey region indicates the burial current direction as inferred by the mean orientation of the felled fronds. **B**, sketch of the Parv Bed showing the relative positions of *Parvancorina*, ‘fronds’ and scourmarks.



Supplementary Figure 2. A, regression of ridge area (mm²) against body area (mm²) shows a strong allometric relationship between the two variables such that the anchor-shaped ridge area decreased proportionally to body area with size. **B,** $\log_{10}$ regression plot of **A**. **C,** regression of *Parvancorina* height (mm) against body area (mm²) reveals that smaller specimens have greater relief for their size compared to larger specimens. We chose *Parvancorina* specimens randomly, originating from nine different localities in the Flinders Ranges. **D,** nearest-neighbour cluster analysis of *Parvancorina* on the Parv Bed. There is some evidence for spatial aggregation between distances of 5 and 17.5 cm, where observed values (black line) > Poisson values (dashed line). We did 99 Monte Carlo simulations (grey shaded region) to reveal no evidence of spatial clustering.

Chapter 5

A new fossil bilaterian from the Ediacaran of the Flinders Ranges, South Australia

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Unsubmitted manuscript

Statement of Authorship

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Principal Author

Name of Principal Author (Candidate)	Felicity J. Coutts		
Contribution to the Paper	Led the research, drafting and finalisation including all figures.		
Overall percentage (%)	75%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	29/01/2019

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Corey J.A. Bradshaw		
Contribution to the Paper	Reviewed paper drafts, provided guidance on writing style and publication format. Helped conduct regression analyses and create figures relating to morphometric analysis. Provided input on content, structure and style of figures.		
Signature		Date	29/01/2019

Name of Co-Author	Diego C. García-Bellido		
Contribution to the Paper	Reviewed paper drafts, provided guidance on writing style and publication format. Provided input on content, structure and style of figures.		
Signature		Date	29/01/2019
Name of Co-Author	James G. Gehling		
Contribution to the Paper	Helped identify new fossil. Reviewed paper drafts, provided guidance on writing style, figures and publication format.		
Signature		Date	29/01/2019

5.1 Abstract

The discovery of a previously undescribed fossil taxon from Ediacara Conservation Park and the National Heritage-listed fossil site Nilpena of the Flinders Ranges in South Australia, presents a body plan previously unknown among the Ediacara biota (c. 555 million years ago). This unique body plan adds to the complexity of taxonomic forms characterising this earliest period of complex life on Earth. The fossil demonstrates basal characters analogous to bilaterians, including bilateral symmetry, anteroposterior and dorsoventral asymmetry. Due to the limitations of Ediacaran fossil preservation, it is difficult to confidently assign this new fossil to any particular phylogenetic group; however, it shares some basic similarities with the Ediacaran stem-group mollusc *Kimberella*. We herein describe the fossil as a possible early stem-group mollusc and as a new genus and species *Velocephalina greenwoodensis* (gen. et. sp. nov.). Further, we suggest that the discovery of this new taxon adds to the mounting evidence of a bilaterian diversification in the late Precambrian.

5.2 Introduction

The Ediacara macrofossils of the Flinders Ranges in South Australia are indirectly dated to around 555 million years ago (Knoll *et al.* 2006; Martin *et al.* 2000) and are among the earliest representatives of complex macroscopic life on Earth (Narbonne 1998; Narbonne 2005; Sprigg 1947). The Ediacara biota were largely soft-bodied and benthic marine multicellular organisms that lived within a wide variety of submarine environments (Clapham *et al.* 2003; Gehling & Droser 2013; Xiao & Laflamme 2008). The unique 'snapshot' preservation style of Ediacaran fossils combined with a lack of vertical bioturbation (Droser *et al*. 2006), provide a glimpse into these ancient marine communities almost as they were in life over large surface areas of seafloor before subsequent burial, compaction, and mineralisation (Gehling 1999; Gehling & Droser 2009). Several phyla have been described from these deposits that predate the Cambrian 'explosion of life', and include what have been regarded as the first putative molluscs (Darroch *et al.* 2015), echinoderms (Gehling 1987), sponges (Clites *et al.* 2012), and arthropods (Glaessner 1980; Lin *et al.* 2006; Zhang *et al.* 2003). These metazoan affinities are contentious, but there are still many morphologically complex forms that have yet to be described formally.

Here we report the discovery of a new Ediacaran fossil taxon with a likely bilaterian affinity. The fossil was originally discovered in the northern part of Ediacara Conservation Park, and more recently at the National Heritage listed fossil site Nilpena in the Flinders Ranges of South Australia. This small, soft-bodied fossil organism (< 2 cm long), shares some similarity with the Ediacaran stem-group mollusc *Kimberella*. However, it presents new characters previously unobserved among Ediacaran taxa, so we describe it herein as a new genus and species: *Velocephalina greenwoodensis*. This fossil was first recognized in a prominent fossil bed described from Ediacara Conservation Park (Coutts *et al.* 2016): NECP Bed-1, and initially it was referred to as ‘Form 1’. Coutts *et al*. (2016) analysed the whole assemblage, and in this article we present a formal description of this new fossil taxon as well as discuss its morphological characters and possible phylogenetic relationships.

Due to taphonomic limitations imposed by Ediacara-style preservation in the Flinders Ranges, descriptions of Ediacaran genera have varied considerably since their original discovery over 60 years ago (Glaessner 1958; Glaessner & Wade 1966; Sprigg 1947). Gradually, we appear to be building a clearer picture of the earliest complex, multicellular life forms present in the late Proterozoic, and in light of recent studies (Gold *et al.* 2015; Lin *et al.* 2006; Rehm *et al*. 2011; Rota-Stabelli *et al*. 2013) and the new taxon we present here, we suggest that bilaterians were likely more prevalent in the late Precambrian than previously thought.

5.3 Geological setting

Ediacara Conservation Park and Nilpena lie on the western margin of the Flinders Ranges (Fig. 1A). Late Ediacaran deposits of the Rawnsley Quartzite outcrop around the periphery of Ediacara Conservation Park, in which the fossil-bearing strata of the Ediacara Member (Fig. 1B) preserve a diverse suite of fossils within delta-front and wave-base facies (Gehling & Droser 2013). Nilpena is a well-established site of extensive Ediacaran research, and exploration of the fossiliferous hills demonstrates wide-ranging, submarine depositional environments preserving Ediacaran fossils (both *in situ* and transported) in shallower shore-face settings through to deeper canyon settings (Gehling & Droser 2013). During the late

Ediacaran Period, the Flinders Ranges was a submarine basin in which Ediacaran communities thrived. Over millions of years, the sediments that now comprise the Flinders Ranges were gradually deposited in this basin. Storms reworked deltas on the basin margins smothering Ediacaran communities that were established below wave-base and delta-fronts, while frondose organisms that were established in shallower settings were torn and transported to deeper water (Tarhan *et al.* 2010; Tarhan *et al.* 2015). The varying intensity of burial currents on Ediacaran communities either resulted in frondose organisms being knocked over before preservation, thus providing a gauge of the burial current's dominant direction (Tarhan *et al*. 2010; Coutts *et al.* 2016), or were torn out from the sediment altogether.

Ediacara-style preservation and some of its elements seems to survive into the Cambrian. A case of this is recognized in the massive sands of the basal Cambrian Uratanna Formation, which fill a channel cut into the underlying Ediacara strata (Fig. 1B). The Parachilna Formation lies above the Uratanna Formation, characteristically preserving *Diplocraterion* burrow beds that demonstrate the advent of bioturbation (vertical burrowing) and the termination of Ediacaran 'mat-ground' life-styles (Gehling 1999; Liu 2016).

The fossiliferous strata of the Ediacara Member in the northern half of Ediacara Conservation Park has produced an abundance of fossil material and preserves a diverse range of fossilized organisms in high resolution (grain size < 100–500 µm; Coutts et al 2016). Fossil surfaces preserve a background of textured organic surfaces (Gehling 1999) of microbial-induced origin (see Gehling 1999; Noffke *et al.* 2001). Specimens are preserved as external moulds, dorsal contours and composite internal structures in the bases of stratified siliciclastic fossil beds. Casts of the original fossils therefore reveal the positive hyper-relief

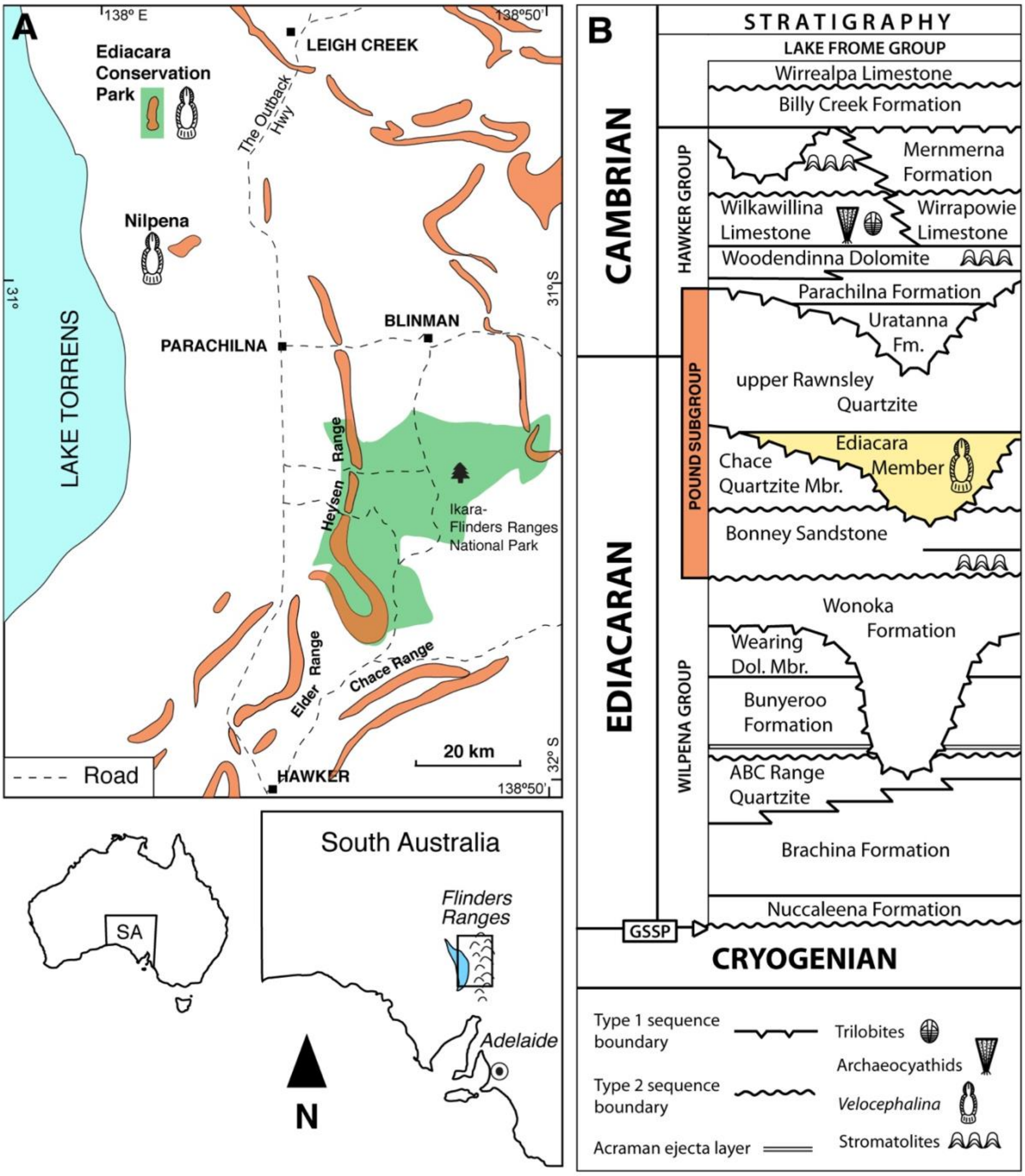


Figure 1. Location and stratigraphic position of fossiliferous Ediacaran outcrops in the Flinders Ranges of South Australia (Australia). **A**, map showing the location of Ediacara Conservation Park where *Velocephalina* gen nov. was found. **B**, stratigraphic chart showing the relative position of the fossiliferous Ediacara Member in the Flinders Ranges. Figure modified from Gehling & Droser (2013) and Coutts *et al*. (2016).

body of the organism after burial, compaction, and fossilisation. The new genus and species is found preserved in beds within the same assemblage as distinctive Ediacaran genera: *Dickinsonia, Kimberella, Parvancorina*, *Spriggina*, *Rugoconites*, *Tribrachidium*, *Yorgia*, *Charniodiscus*, and *Praecambridium* (Coutts *et al.* 2016).

5.4 Materials and methods

All fossils are housed in the South Australian Museum palaeontological collections and catalogued under SAM P numbers. The fossil impressions were initially observed on a large contiguous fossil bed in North Ediacara Conservation Park (NECP Bed-1), previously assembled in 2013, and later identified on several ‘float blocks’ that likely originated from the same bed (Coutts *et al.* 2016). Additionally, a single specimen was discovered at Nilpena. In total, 14 specimens have been identified and featured here. We used a combination of low-angled light and *Silly Putty*® to identify the fossil specimens that were later transported back to the South Australian Museum for analysis. We recorded the orientations relative to current direction for NECP Bed-1 specimens *in situ*. After cleaning the fossils to remove superficial sand and silt, we made casts of individual specimens using various casting material media, including latex dyed black with Indian ink, black two-part liquid putty and *Pinkysil*® putty (Barnes brand). Due to inter-specimen taphonomic variation, using different casting mediums (providing different qualities) appeared to maximise the overall number of observable features. We measured and made morphological observations from the casts of the original fossils under magnification, and took photographs using a Canon EOS 50D camera with a Canon MP-E 65 mm macro lens. We analysed these measurements using R (R Core Team 2018). A 3-D reconstruction of *Velocephalina greenwoodensis* gen. et sp. nov. was created using the program *Zbrush*® version 4R6.

5.5 Systematic Palaeontology

Genus ***Velocephalina*** gen. nov.

Type and only known species. *Velocephalina greenwoodensis* sp. nov.

Diagnosis. As for the species.

Etymology. *Velocephalina*: Greek, from *velos* (*βελος* = arrow) and *cephalos* (*κέφαλος* = head), after the shape of the anterior part of the body.

Velocephalina greenwoodensis sp. nov.

(Figs 2A–N, 3, 4)

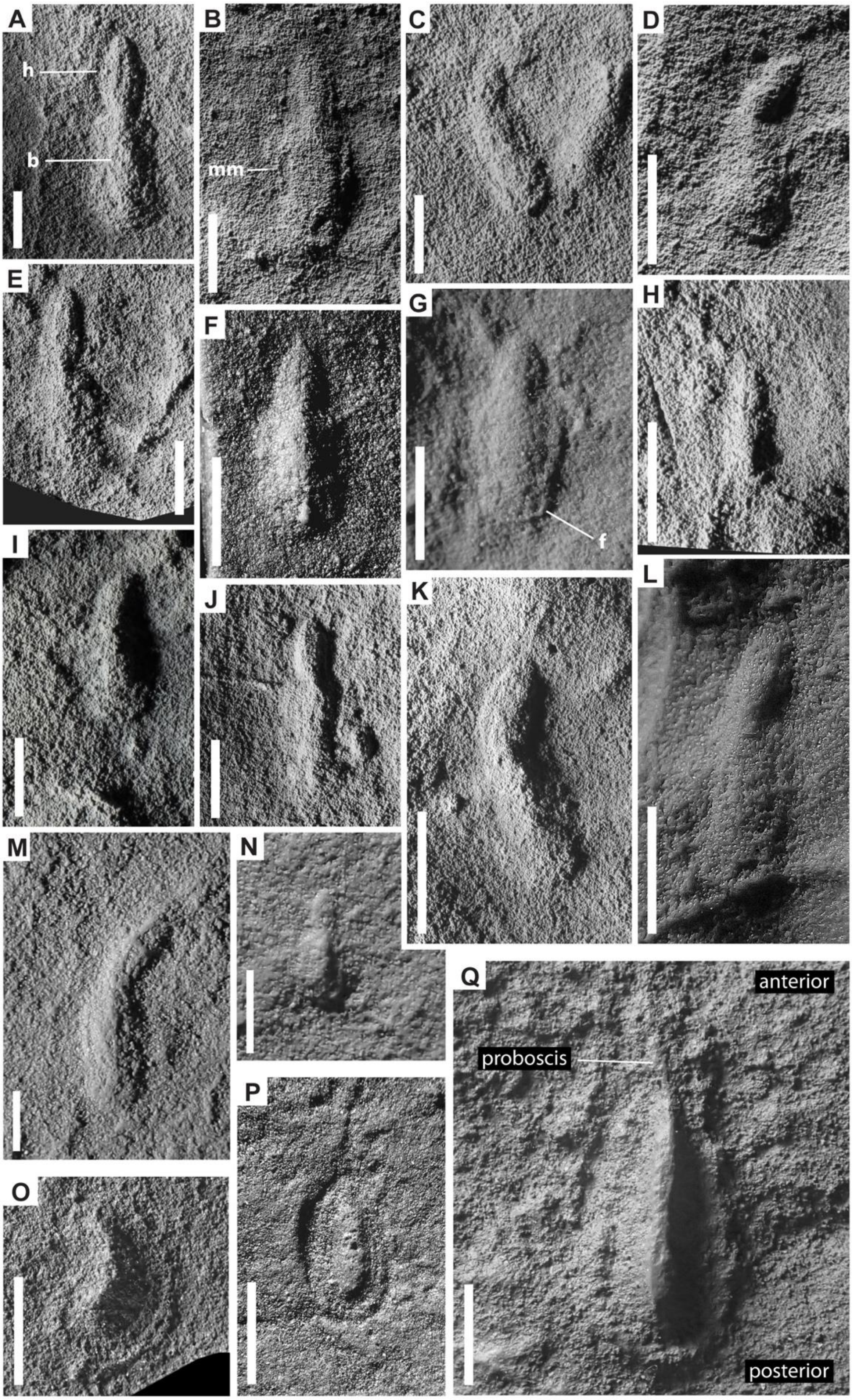
Etymology. After the landmark Greenwood Cliff, a few tens of metres from the site where the fossil was found.

Holotype. Complete specimen, SAM P55687. Latex cast illustrated in Fig. 2A7.

Paratypes. Thirteen other specimens: SAM P55674, SAM P55671, SAM P55685, SAM P55672, SAM P55673, SAM P55680, SAM P55686, SAM P55676, SAM P55675, SAM P55678, SAM P55681, SAM P55670 and SAM P55669.

Stratigraphical range. Ediacara Member of the Rawnsley Quartzite, Pound Subgroup.

Type locality. Northern section of Ediacara Conservation Park, Flinders Ranges, South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proboscis
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Figure 2. *Velocephalina greenwoodensis* new gen. and sp., and *Kimberella quadrata* from Ediacara Conservation Park and the National Heritage listed fossil site Nilpena. **A–N**, latex casts of type specimens of *Velocephalina greenwoodensis* new gen. and sp.: (A) SAM P55674, (B) SAM P55671, (C) SAM P55685, (D) SAM P55672, (E) SAM P55673, (F) SAM P55680, (G) Holotype, SAM P55687, (H) SAM P55686, (I) SAM P55676, (J) SAM P55675, (K) SAM P55678, (L) SAM P55681, (M) SAM P55670, (N) SAM P55669. **O–Q**, latex casts of *Kimberella* specimens: (O) GWR01 ECP-15, (P) N09-18, (Q) D127 S31 chosen for their comparable size to *Velocephalina* [*Kimberella* could grow to > 10 cm long]. Abbreviations: **h**: head, **b**: body, **mm**: mantle margin, **f**: flange Scale bars: 5 mm.

Australia, Australia.

Diagnosis. Low-relief, elongate and bilaterally-symmetrical organism with axial and dorsoventral differentiation. Body consists of two distinct longitudinal portions: arrowhead-shaped component separated by narrow constriction from larger, convex, ovoid component. Arrowhead-shaped component is flanked by crenelated rim and occasionally presents axial groove. Body surrounded by underlying peripheral rim and often terminated in flat, spatula-shaped ‘flange’.

Description. Fossil specimens are < 1 mm in relief, ranging from 6.4 to 17.6 mm in overall length, and from 2.7 to 5.5 mm at the widest point. The arrowhead component, or ‘head’, ranges from 2.2 to 7.2 mm in

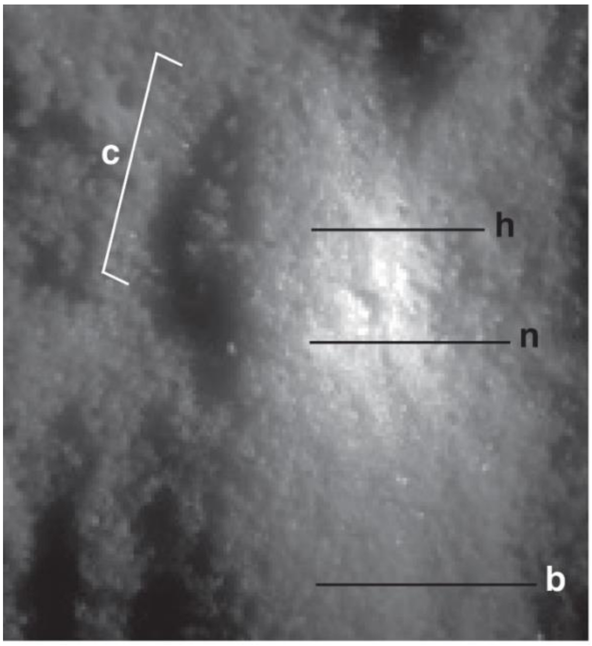

Figure 3. Detail of *Velocephalina greenwoodensis* gen. et. sp. nov.. **A**, head showing lateral crenellations along its sides (Holotype, SAM P55687). **B**, Head of the same fossil showing the axial groove extending two thirds of the sagittal length. **C**, abbreviations: **cr**: crenellations, **h**: head, **b**: body. Scale bar: 2.5 mm.

length and 1.5 to 3.3 mm in width, while the convex, ovoid portion, or ‘body’, ranges in length from 4.6 to 10.4 mm. The terms ‘head’, ‘neck’ and ‘body’, and the relative anterior-posterior orientation, are used to facilitate description and discussion, and should not to be taken as statements of homology with these structures in metazoans. Similarly, when indicating dorsal and ventral position, it will refer to such positions in the positive latex cast and the original organism rather than the fossil, which is a negative mould. The fossil appears to have at least two levels, dorsoventrally: (*i*) a dorsal component consisting of the head, body, and possible mantle margin (see Fig. 2A, B), and (*ii*) a basal layer of tissue that appears as a rim around the periphery of the organism, which we interpret as a possible muscular foot (Figs 2 and 4). The head is somewhat shaped like an arrowhead, tapers distally and is separated from the main body by a narrow constriction, or neck ≤ 1 mm wide.

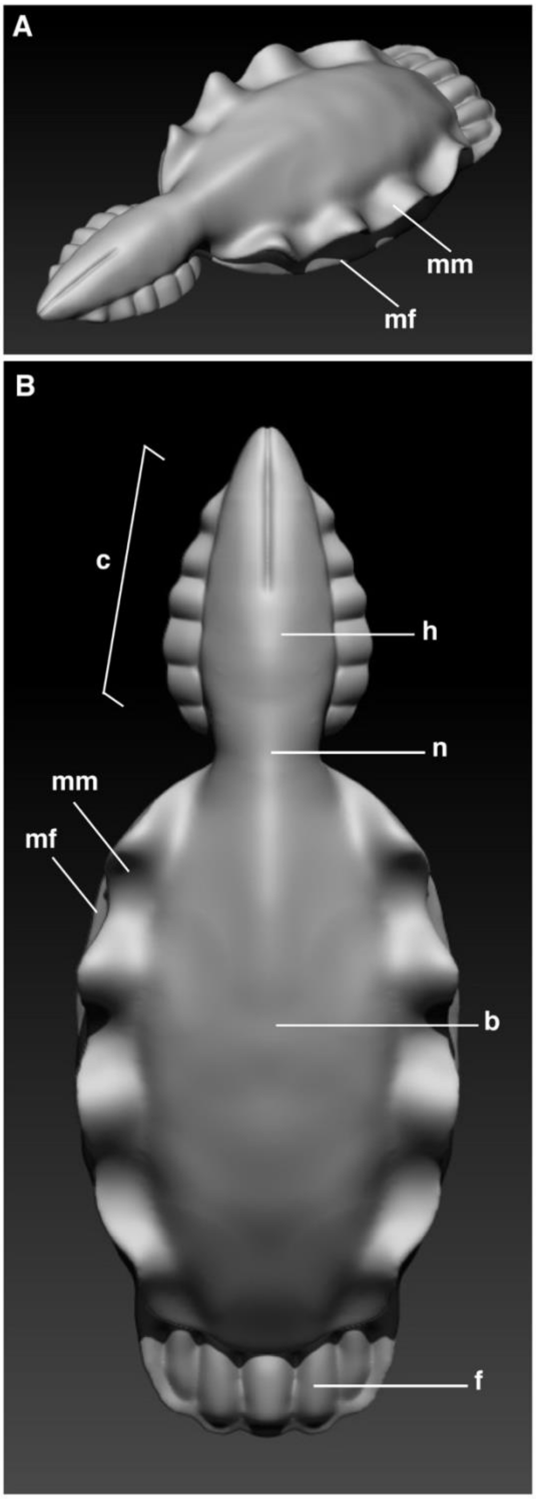

Figure 4. 3-D reconstructions of *Velocephalina greenwoodensis* new gen. and sp. **A**, angled side view of fossil illustration. **B**, dorsal view of fossil illustration. Abbreviations: **b**: body, **cr**: crenellations, **f**: flange, **h**: head, **mf**: muscular foot, **mm**: mantle margin, **n**: neck. Artwork by Katrina Kenny.

A medial groove in the dorsal side of the arrowhead component is evident in six specimens, starting in the distal end and terminating one-half/two-thirds toward the body. A peripheral rim flanking the sides of the 'head' appears to be decorated with at least six lateral crenellations per side (Fig. 3 and Fig. 4). A 'flange' of ventral origin appears from beneath the posterior end of the 'body', and underlaps the lateral rim around the organism. The 'flange' appears to have ≥ four, evenly-spaced longitudinal grooves, and in the holotype is almost spatula-shaped (Fig. 2G).

Morphological analysis. After compiling the body dimensions of the 14 specimens, we scaled and centred these values to compare the linear relationship between the length and width for (*i*) the whole organism, (*ii*) the main 'body' only, and (*iii*) the 'head' only. We hypothesised that if the body components differed in relative growth rate across the size range of the preserved specimens, the scaled length-width relationships would demonstrate different slopes. We compared the length-width relationships of *Velocephalina* to those of the Ediacaran putative stem-group mollusc *Kimberella* (because this is the closest analogue for comparison), to examine whether there were any similarities in growth form between the two species.

5.6 Results

The confidence intervals of the slope of scaled length-width relationships for the whole organism (Fig. 5A), 'body' only (Fig. 5B), and 'head' only (Fig. 5C) all overlapped.

Expressing the relationships as scaled ratios of length:width between the whole organism and the 'body' (Fig. 6A) or the 'head' only (Fig. 6B), supported the view that no differences in growth form between the different components could be detected with the sample available. Likewise, we found no evidence for a slope difference between the whole-organism length:width relationships between *Velocephalina* (Fig. 6C) and *Kimberella* (Fig. 6D).

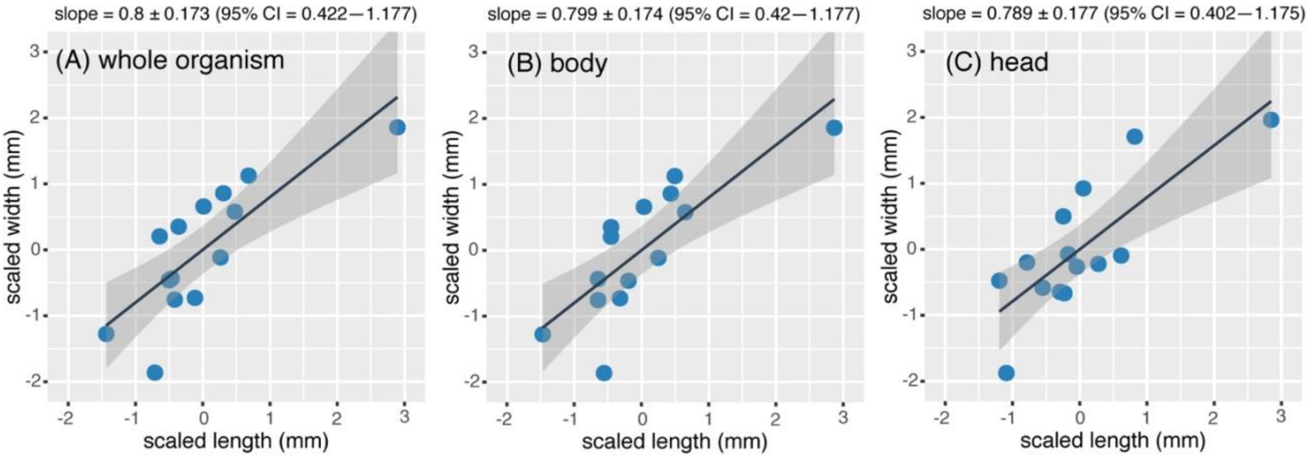

Figure 5. Morphometric relationships between length and width of *Velocephalina* specimens. Least-squares relationship between length and width of the (**A**) whole organism, (**B**) body and (**C**) head in mm (scaled and centred data), plus the 95% confidence interval (CI) of the slope for each is shown.

All *Velocephalina* specimens are consistently preserved with the same observable characters (bilateral symmetry, anteroposterior and dorsoventral differentiation) and are thus not likely to be transported before preservation. Although we use the terms 'head', 'anterior' and 'posterior', we cannot yet confidently establish the true direction of the organism due to the lack of trace fossils associated with *Velocephalina* preventing the unequivocal identification of the anterior and posterior ends of the organism. Specimens from NECP Bed-1 showed a slight bias in orientation (Fig. 7), and although the sample size was small, an association between orientation and burial current direction should be noted (mean orientation = 5.5°; see Fig. 7B). There was no morphological evidence to suggest that the fossil organism was attached to the seafloor. We observed no distinct spatial associations with other taxa.

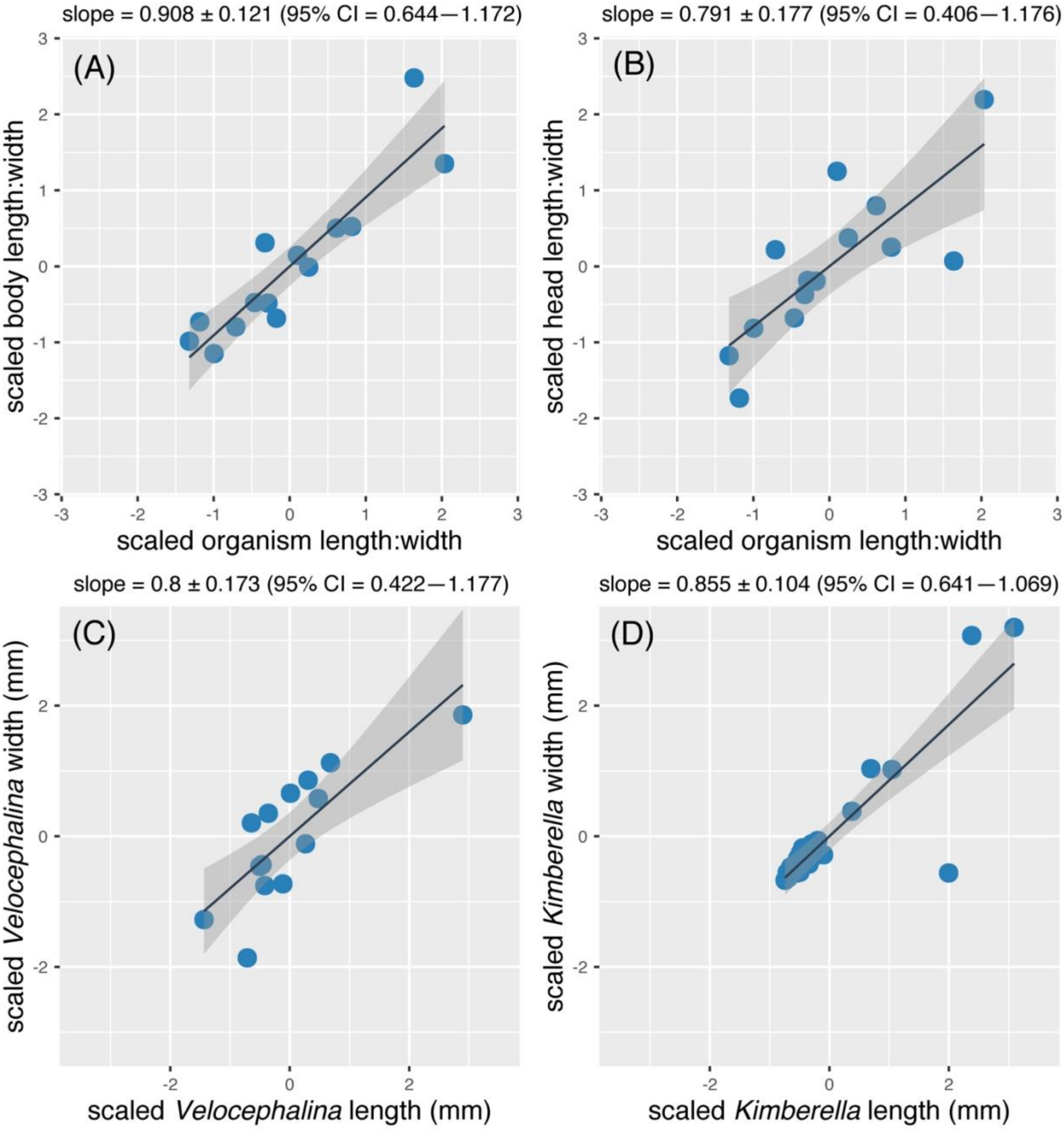

Figure 6. Scaled and centred ratio of length:width for the whole organism *versus* that for (**A**) the body and (**B**) head only (95% confidence interval [CI] also given). Also shown is the length:width relationship for the whole organism of (**C**) *Velocephalina* and (**D**) *Kimberella* for comparison.

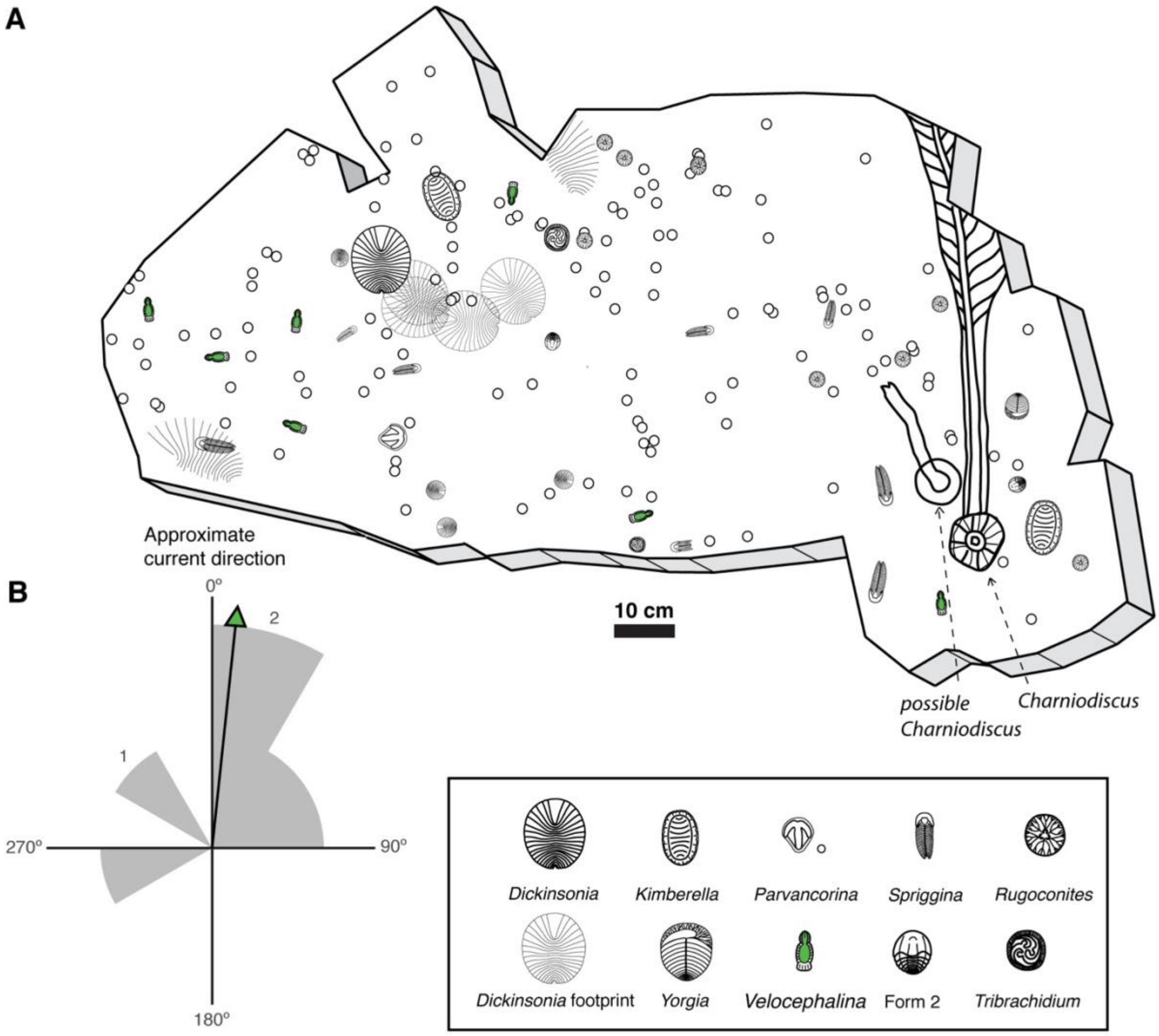

Figure 7. Relative spatial distribution and orientations of *Velocephalina* within the preserved community on NECP Bed-1. **A**, sketch of the latex cast of NECP Bed-1 showing the relative position of specific Ediacaran taxa within the community. *Velocephalina* specimens are highlighted in green. The burial current direction is indicated by the felled 'frondose' fossil *Charniodiscus*. See *Methods* in Coutts *et al.* (2016, 2018) for more details on the data collection and analysis of NECP Bed-1. **B**, rose diagram of *Velocephalina* orientations on NECP Bed-1. Approximate burial current orientation given by black arrow. Mean *Velocephalina* specimen orientation indicated by green arrow (5.5° E from estimated burial current direction).

5.7 Phylogenetic considerations

Among moving animals, the gross characters of bilateral symmetry and anteroposterior differentiation is widespread (Droser *et al.* 2002), a fundamental feature among bilaterians (Finnerty 2003) allowing for directed movement. Thus, the bilateral symmetry and the anteroposterior and dorsoventral differentiation observed in *Velocephalina greenwoodensis* gen. et. sp. nov. suggest placement within the clade Bilateria. It is uncertain to which taxonomic group this fossil organism belongs, because not enough unequivocal anatomical characters are present to place it definitively within a phylum. This is partially due to the almost two-dimensional nature of Ediacaran fossil preservation that rarely shows both sides of an organism, obscures the various body levels and the grain-size makes observing small anatomical characters challenging. However, we can make inferences about the shape and contours of a fossil and discuss how these features might relate to extant organisms or fossils for which affinities are better known.

One could interpret the body of *Velocephalina* as longitudinally tripartite (divided into three parts), a body plan that resonates with the hemichordates, for which some representatives have been reported in the Cambrian (Nanglu *et al*. 2016). However, on closer inspection, the longitudinal divisions might also be associated with the dorsoventral morphology. Hemichordates tend to have tubular bodies, with minimal external evidence of a dorsoventral axis (Cameron 2005). The externally undifferentiated dorsoventral axis in hemichordates is a consequence of their tube-dwelling lifestyle, whereas in non-burrowing epibenthic organisms, dorsoventral differentiation is expressed further in the functional morphology of the organism, as is the case with *Velocephalina*.

Comparing the smooth convex body shape, the anterior arrow-shaped portion of the body, the crenellated rim, and the possible muscular foot in *Velocephalina* with the Ediacaran presumed stem-group mollusc *Kimberella* can help assess how the preserved morphology of *Velocephalina* fits the profile of a mollusc-grade organism. If *V. greenwoodensis* was indeed a primitive representative of the diverse group Mollusca, it should display basic characters typical of the whole group, such as an unsegmented body with bilateral symmetry, an internal or external shell (although this feature is lost completely in some groups), a toothed, chitinous microscopic tongue (radula), a dorsal mantle, and a muscular foot (or tentacles) (Moore & Pitrat 1960). While many of these characters are not strictly identifiable in *Velocephalina*, we can make inferences based on the characters available and also its similarities to the mollusc-grade fossil *Kimberella*. Both *Kimberella* and *Velocephalina* display bilateral, anteroposterior and dorsoventral differentiation (basic characters of animals). However, three characters distinguish these taxa: (1) all *Velocephalina* specimens have a constriction or a sort of 'neck' subdividing the two main body components, while *Kimberella* has an ovoid body shape, occasionally presenting a small, anterior protuberance, (2) the presence of a terminal flange in *Velocephalina*, and (3) *Kimberella* specimens appear to have an uninterrupted rim of consistent thickness that surrounds the periphery of the fossil (Fig. 2O–Q). The reference to a 'head' and a 'neck' in the new taxon should not be taken as a claim that *Velocephalina* had any degree of cephalization in this terminal body part, only that its differentiation from the 'body' would probably confer some degree of functionality. The terminal 'flange' appears to be of ventral origin, which we suggest could be associated with an underlying muscular foot.

The medial groove of *Velocephalina*'s head is perhaps comparable to the anterior protuberance of *Kimberella* specimens, the latter feature being generally regarded as a proboscis (see Fig. 2O) that is often associated with paired feeding-scratch traces called *Kimberichnus* (Gehling *et al.* 2014; Ivantsov 2009). However, the arrowhead of *Velocephalina* is always present and consistent in shape, whereas the proboscis in *Kimberella* appears to have been somewhat retractable and was invariably housed beneath the mantle of the organism (Fedonkin & Waggoner 1997). Furthermore, no trace fossils have been associated with *Velocephalina* as yet. This could either be a result of the diminutive size of the fossils and thus any trace fossils present would not be resolvable, or simply because it did not produce any. Juvenile *Kimberella* specimens, some smaller than *Velocephalina* (see Fig. 2Q), clearly maintain the morphology seen in the large specimens, and *Velocephalina* can therefore be ruled out as a juvenile morph of *Kimberella*.

Among modern taxa, *Velocephalina* is possibly comparable to the mollusc group Gastropoda (Heterobrancha), mostly by the possible presence of a ventral muscular foot beneath a soft, shell-less mantle and the crenellated mantle margin. Superficially, these characters resonate with the Nudibranchia, although diversification of this group was apparently a comparably recent event (Wollscheid-Lengeling *et al.* 2001). The actively carnivorous nudibranch *Melibe viridis* can be compared to *Velocephalina*, with the former having specialized mouth-parts that resemble the arrowhead-shaped head in *Velocephalina*. *Melibe* has an extendable oral ‘veil’ or ‘hood’ that balloons outwards to encapsulate moving prey. Then, as the oral hood collapses to trap the prey, it closes in from the sides, resulting in a sub-rounded shape with a medial groove (Allan 1932; Eyeseawonders 2011; Gosliner & Smith 2003; Rang 1829). Likewise, the medial groove in *Velocephalina* could have been created by specialized tissues that were capable of separating for a particular function (e.g., feeding) and retracting for periods of rest or movement. It is possible that the apparent dorsal location of the medial groove in *Velocephalina* could conceivably be a ventral feeding structure that has been preserved through the dorsal compression of the organism.

Alternatively, *Velocephalina* could be comparable with the phylum Platyhelminthes (flatworms), and in particular the subgroup Turbellaria. The oldest fossil specimens of Turbellaria are dated to about 40 million years ago (Poinar, G. Jr. 2003), although others have suggested that Turbellaria made its appearance during the rapid phylogenetic radiation of the ‘Cambrian explosion’ (Carranza, Baguñà) ~ 541 million years ago (Knoll & Caroll 1999). However, molecular-clock estimates place the group as paraphyletic, i.e., not sharing a common ancestor with bilaterians. Living Turbellaria are generally sub-rounded to elongated in shape with a distinct head end and pseudotentacles; however, these are not always well defined and intra-species body shape variability is high (Higley 1917). Furthermore, all *Velocephalina* specimens discovered so far generally tend to display structural consistency in their shape, repetition of features, and lack the morphological flexibility demonstrated by living Turbellaria, and a key feature of Platyhelminthes.

The external contours of *Velocephalina* are also comparable to the generalized profile of a cephalopod. However, based on the consistent preservation of its characters, *Velocephalina* was benthic. Furthermore, the lack of preserved details that are normally consistent with cephalopods such as anterior tentacles, defined lateral fins, and an anterior ventral siphon reject the classification at this stage.

The presence of the Ediacaran stem-group mollusc *Kimberella* is evidence that complex bilaterians of molluscan grade lived during the Ediacaran (Vinther & Smith 2015), and suggests that other mollusc-grade organisms might have also existed at this time. Furthermore, the Mollusca was the most diverse phylum in the early Palaeozoic (Sepkoski

1979) with a rich fossil history. It is therefore likely that members of the Mollusca or at least the superphylum Lophotrochozoa (in which the Mollusca is included) were present in the late Ediacaran (Fedonkin & Waggoner 1997; Valentine 1994), but were perhaps not readily preserved (Budd & Jackson 2016).

5.8 Conclusion

The new Ediacaran fossil *Velocephalina greenwoodensis* we propose shows bilaterian characters of possible molluscan grade. The generalised body plans observed among the Turbellaria (Platyhelminthes) and Mollusca (i.e., gastropods, bivalves and cephalopods), appear to reflect more closely that of *Velocephalina*; however, its true biological affinities remain unclear. The discovery of this diminutive taxon, not long after detailed observation of large surfaces from North Ediacara Conservation Park began, suggests not only that bilaterians were likely more common within the Precambrian than previously known, but also that further in-depth analysis of these fine-grain fossil surfaces could potentially reveal morphologically unique new groups of organisms and genera.

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Chapter 6

Rules of ecological community assembly unchanged for over half a billion years

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Name of Principal Author (Candidate)	Felicity J. Coutts		
Contribution to the Paper	Provided input to the research, writing, drafting and finalisation including figures and tables.		
Overall percentage (%)	55%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	29/01/2019

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	Reviewed paper drafts, provided guidance on writing style and provided guidance on content.		
Signature		Date	29/01/2019

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Signature		Date	29/01/2019

6.1 Abstract

The unique ‘snap-shot’ preservation of Ediacaran communities (ca. 575—542 Mya) in vast surface areas of fossilised seafloor provides an exceptional opportunity for examining the ecological patterns of Earth’s earliest multicellular life. The power-law form of the species-area-relationship ($S = cA^z$) — where species richness (S) accumulates over landscapes as a power function (z) of increasing area (A) — is regarded as one of the few fundamental laws of ecology. This same model has been applied to examples of most living communities, where z lies predictably between 0.2 and 0.4, with the central tendency at the ‘golden’ value of 0.32 (SD = 0.16). To test if the same ecological assembly rule describes the earliest complex communities on Earth, we applied the species-area model to 18 fossil beds from the National Heritage-listed Ediacaran fossil site Nilpena in the Flinders Ranges of South Australia, totalling 138 m^2 of preserved Ediacaran seafloor with > 2000 individual fossil organisms in 31 genera. Remarkable preservation, a lack of pre- and post-burial bioturbation, and a deep understanding of these beds’ taphonomy allowed us to compile reliable species-area data. Remarkably, we show that these Ediacaran communities followed a similar ecological assembly rule as living communities, with $\bar{z}$ = 0.35 (SE_z = 0.11). Despite a lack of evidence for predation in these earliest animal communities, ecological community-assembly rules appear to have persisted throughout most of evolutionary history despite vast changes in species composition.

6.2 Introduction

Inferring ecological patterns of life that existed deep in geological time is a challenge given the incomplete nature of the fossil record, the snapshot preservation of specimens often in non-living positions, and the limitations when interpreting taphonomic disturbance (Glaessner & Daily 1959; Gehling 1991; Kidwell 2001; Tarhan *et al*. 2010; Liu *et al*. 2011). However, the unique preservational mode of Ediacaran fossil seafloors (ca. 555 Ma) presents whole communities virtually 'frozen in time', including organisms that were living and dead at the time of burial (Gehling 1991; Liu *et al*. 2011; Coutts *et al*. 2016). Further, the lack of sediment bioturbation of Ediacaran seafloors and the *in situ* arrangement of organisms preserved 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.

Community-assembly rules govern all living ecosystems, and are important assessment tools used to measure fundamental components of ecological communities (Giam *et al*. 2011). Due to the immense age of Ediacaran soft-bodied communities, and apparent lack of predation, one might not expect them to demonstrate the same ecological assembly rules as living communities. Predation has long been considered a regulatory mechanism for community composition, although the extent of its influence is still uncertain (Chase *et al.* 2002). For example, predation can influence interspecific competition, and either promote stability in high-productivity environments, or conversely increase extinction risk in low-productivity environments (Chase *et al*. 2002; Ryberg & Chase 2007). While evidence of predation is largely absent from the Ediacaran fossil record, intra- and interspecific competition is evident in the form of tiered growth programs (Clapham & Narbonne 2002), ecological niche partitioning (Bambach *et al*. 2007), and reproductive dispersal patterns (Droser & Gehling 2008; Mitchell *et al*. 2015). Furthermore, a recent ecological analysis by Finnegan *et al*. (In press) revealed that Ediacaran seafloor communities showed qualities of competition-dominated systems, reflective of modern communities (Hautmann 2014).

The power-law form of the species-area relationship (SAR), $S = cA^z$, is widely considered a fundamental law in ecology and describes how the number of species (*S*) increases as a power function (*z*) with increasing habitat area (*A*) (Watson 1835, 1859, *in* Triantis *et al*. 2012; Schoener 1976; Dodds 2009). In living communities, the *z* exponent generally lies between 0.2 and 0.4 (MacArthur & Wilson 1967; Rosenzweig 1995). However, a large-scale SAR metadata analysis by Triantis *et al*. (2012) discovered that living communities predictably share a 'golden' *z* exponent of 0.32 ± 0.164 (± SD). The species-area relationship is derived from the theory of island biogeography, where increasing habitat availability progressively leads to higher species richness until the latter reaches an (often theoretical) asymptote (MacArthur & Wilson 1967).

In this paper we hypothesize that Ediacaran communities demonstrated ecological assembly rules that differ from those of living communities given their relatively simple composition, low alpha diversity (but high beta-diversity — Finnegan *et al.* In press), and lack of a predatory guild. To test this, we applied the ubiquitous power-law form of the species-area relationship, $S = cA^z$, to 18 Ediacaran fossil communities from the National Heritage-listed fossil site Nilpena in the Flinders Ranges of South Australia. Altogether, we consider 138 m^2 of fossil seafloor containing > 2000 fossilized Ediacaran organisms belonging to 30 different genera/discrete forms. Here, we are considering the Ediacaran fossil beds from Nilpena, with their discrete boundaries, as independent 'islands' from which we derive a distribution of richness and size estimates to test their fit to the power-law species-area relationship.

6.3 Geological setting

Over the last > 20 years, Nilpena has been a major source of Ediacaran palaeontological research and contains Ediacaran fossils of exceptional preservation and global significance (Droser *et al*. 2006; Gehling & Droser 2013). The Flinders Ranges demonstrates some of the best records of Precambrian stratigraphy and contains the global type section for the beginning of the Ediacaran Period (Knoll *et al*. 2006). Ediacaran deposits are found within

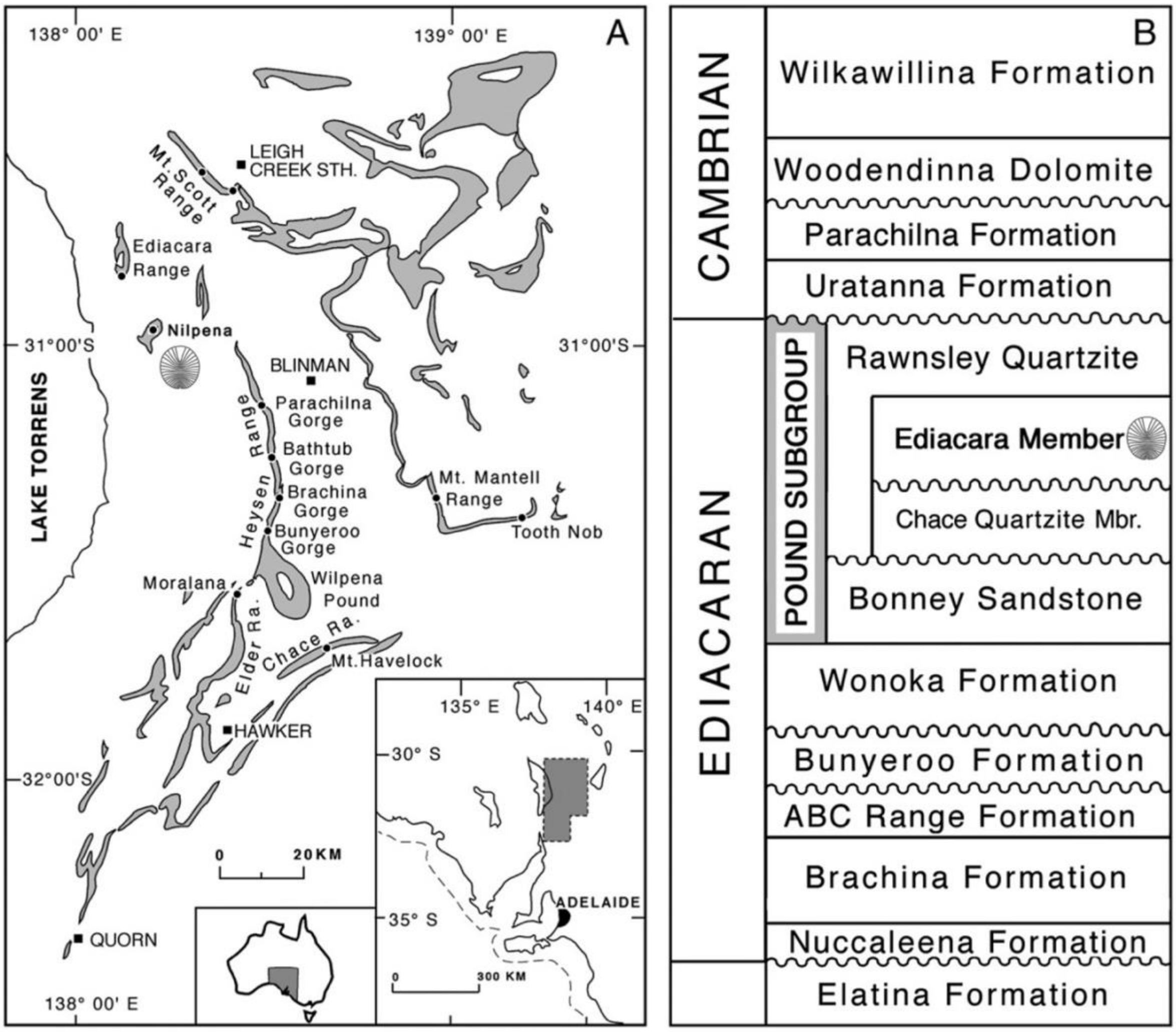

Figure 1. (A) Geographic map of the Flinders Ranges in South Australia, highlighting the Pound Subgroup which contains the fossiliferous Ediacara Member. **(B)** The Ediacaran and early Cambrian stratigraphy of the Flinders Ranges. The National Heritage Listed fossil site Nilpena (A) and the fossiliferous Ediacara Member (B) is marked with a symbol of the iconic Ediacaran fossil *Dickinsonia*. Figure modified from Gehling & Droser (2009).

the Pound Subgroup of the Rawnsley Quartzite (shaded sections in Fig. 1), and outcrop as well-exposed strata throughout the Flinders Ranges.

The marine fossil communities sampled from Nilpena (Fig. 1) are preserved in thinly bedded rippled quartz sandstone and contain well-known taxa such as *Dickinsonia, Spriggina*, and *Parvancorina* (Fig. 2), as well as many other known and undescribed forms. These benthic communities lived in shallow marine environments ranging between fair-weather submarine environments through to below the storm-wave base in deltaic, upper

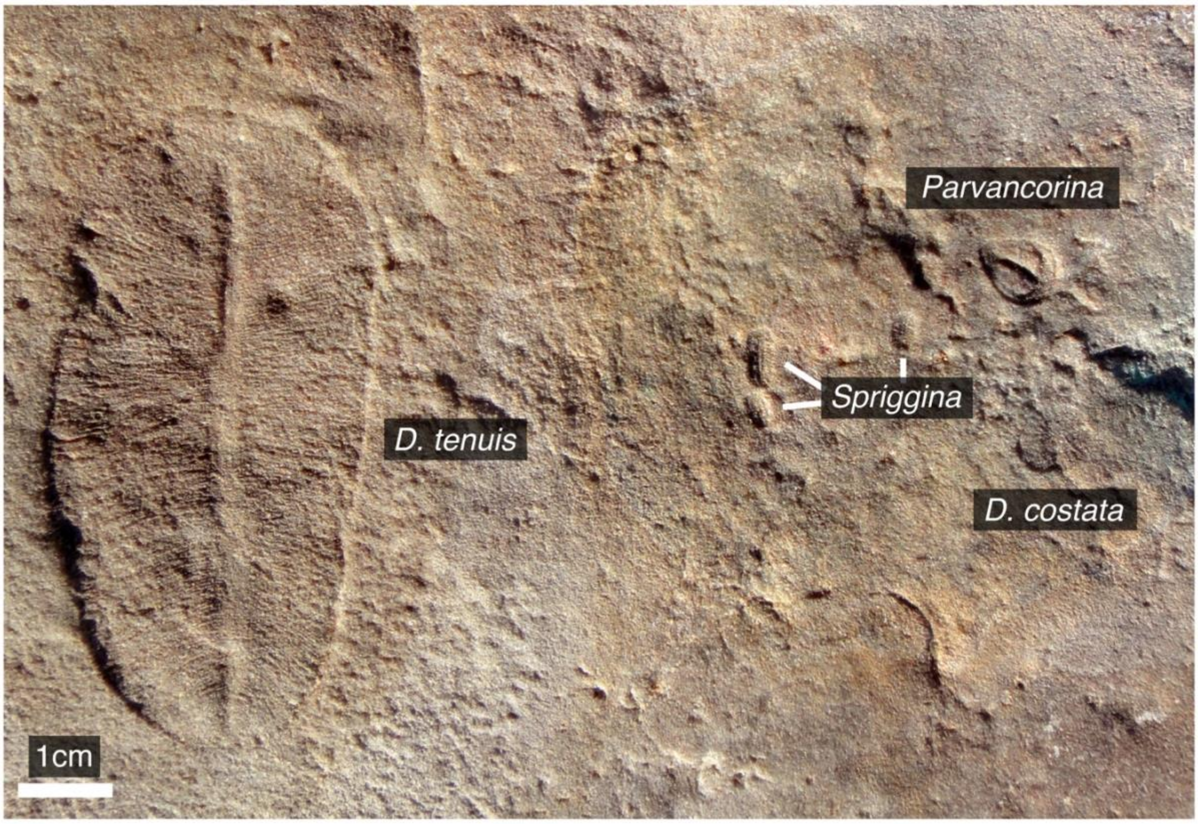

Figure 2. Example of a small Ediacaran fossil cluster on 1TF. Two *Dickinsonia* specimens (*D. tenuis* and *D. costata*), three *Spriggina* specimens (*S. floundersi*) and one *Parvancorina* specimen (*P. minchami*) are present.

and lower canyon-fill settings (Gehling & Droser 2013; Tarhan *et al*. 2017). Ediacaran communities were preserved by waning storm surges that systematically smothered and buried the communities in layers of sand (Gehling 1999). Textured organic surfaces (Gehling 2009) of bacterial or algal origin covered Ediacaran seafloors and aided in the exquisite preservation of these communities (Gehling 1999). Subsequent diagenesis, uplift and exposure of these sedimentary layers have created perfect examples of which to study the earliest examples of complex multicellular communities *in situ*.

6.4 Materials and methods

6.4.1 Data collection

We sourced fossil composition and distribution data from 18 fossil beds, totalling 138 m^2 of fossilized Ediacaran seafloor that collectively contained > 2000 individuals from 30 different genera or unique identified forms. Identifying Ediacaran species can be difficult given the limited preservation of characters available for identification. As a result, many Ediacaran forms still lack an official genus and species title, despite their identification as unique and discrete forms. Many Ediacaran organisms are identified to the genus level only; therefore, we lumped any species into their respective genera for the purposes of this analysis. We sourced the relevant beds from five different sites across the National Heritage Listed fossil site Nilpena: 'Tennis Court' (TC), 'South Tennis Court' (STC), 'One Tree Hill' (1T), 'Plinth' (P) and 'West Side' (Supplementary Table 1; Droser *et al*. 2019).

Over many years, fossil beds from Nilpena have been excavated, cleaned, fossil specimens marked and labelled, and the locations of all organisms recorded (Droser *et al*.

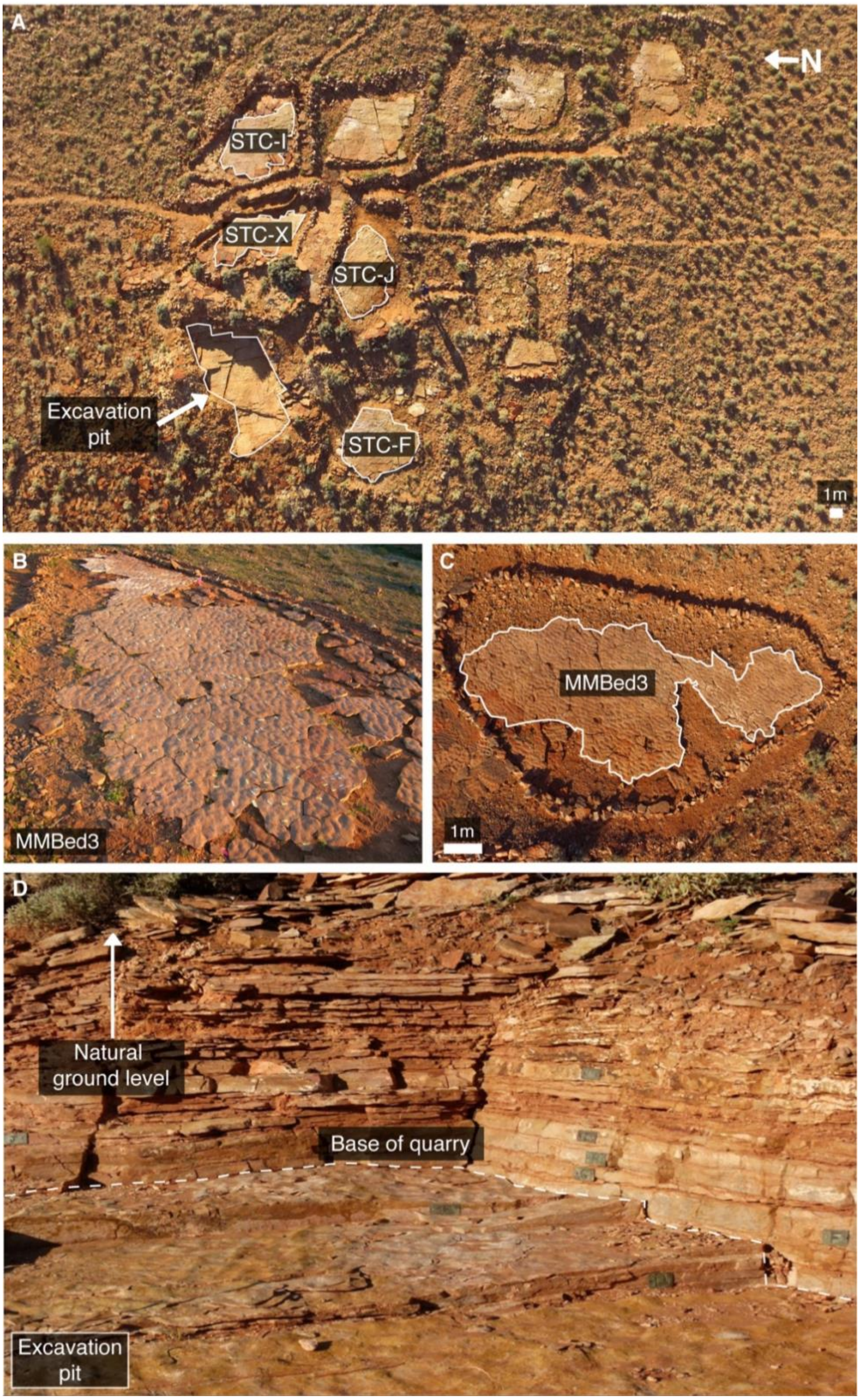

Figure 3. Nilpena fossil beds included in this study. **(A)** Aerial perspective of excavated 'South Tennis Court' (STC) fossil beds at Nilpena. Beds featured here were excavated from the Excavation pit. **(B)** MMBed3 from the TC site in Nilpena with individual specimens marked and labelled with tickets. **(C)** Aerial view of MMBed3. **(D)** STC Nilpena Excavation pit, where many fossiliferous Ediacaran beds have been sourced from (see A).

2019). We included fossil surfaces identified from the Oscilliation-Rippled Sandstone (ORS) Facies and Planar-Laminated and Rip-Up Sandstone (PLRUS) Facies (see Supplementary Table 1), with sedimentary deposition occurring between fair-weather and wave-base submarine environments through to the sub-wave base in upper-canyon environments (Gehling & Droser 2013; Tarhan *et al*. 2017). We excluded fossil beds where there was evidence of more than one community apparent (i.e., reflecting some time-averaging). This ensured a more conservative bed-sampling approach and that our analysis consistently included single communities only.

To measure beds accurately, we took aerial photographs of the fossil beds using a DJI Phantom 3 Standard drone (Figure 3A).

6.4.2 Analysis

We used the R environment for statistical computing (R Core Team 2018) to analyse the data. We first plotted $\log_{10}$ *area* against $\log_{10}$ *richness* to test whether there was evidence for a positive relationship between these two parameters, by comparing it to an intercept-only (null) model (i.e., richness invariant with area). Evidence for a linear relationship on the log-log scale indicates the expected species-area function $S = cA^z$. We compared the two models based on Akaike's information criterion corrected for small samples (AIC_c) (Burnham and Anderson 2002) that penalises the model's likelihood for the number of parameters. We derived AIC_c weights ($wAIC_c$) for each model as an estimate of the relative probability of each, and then calculated the information-theoretic evidence ratio of the SAR power-law *versus* the null model as $wAIC_c$ [SAR] / $wAIC_c$ [null].

Ediacaran *versus* modern communities. We resampled the estimated *z* exponent derived from the Ediacaran SAR model above using a Gaussian sampler and its estimated standard deviation 10,000 times to calculate lower and upper quartile confidence bounds. We did a similar Gaussian resampling of the meta-analytically derived $z = 0.32$ (± 0.164) estimate for modern communities from Triantis *et al.* (2012) as a comparison.

6.5 Results

There was strong evidence for a non-random power-law relationship between Ediacaran richness and area $S = cA^z$ as determined by the high support for the log-log model relative to the null (evidence ratio [*ER*] = 50.4; $R^2 = 0.42$; Fig. 4A; Table 1). As surface area increased, species diversity also increased with a $\hat{z}$ exponent of 0.35 ($SE_z = 0.11$) (Fig. 4B). Although there was some expected uncertainty in $\hat{z}$, the median value of 0.35 (Fig. 4B) is remarkably similar to that of living communities, the latter of which typically lies between 0.2 and 0.4 (0.32 ± 0.16) (Triantis *et al*. 2012). Furthermore, the Gaussian-resampled envelopes from the Ediacaran SAR and the Triantis *et al*. (2012) meta-analytical estimates overlapped near perfectly (Fig. 4C).

Fossil beds (such as 1T-LS, Sub, 1T-NA and B-ARB) where species richness is high and the fossil bed surface area is comparatively small occupy the bivariate space above both simulation envelopes (Fig. 4C). In contrast, fossil beds with a considerably lower species richness plot below the simulation envelope (e.g., Gully and BS-1). Bed taxonomic heterogeneity has been associated with microbial mat maturity, both of which were possibly regulated by the timing of sediment deposition affecting community-development time (Gehling 1999; Droser *et al*. 2019).

Table 1. Comparing model performance between the power-law species-area relationship (SAR) and the null (intercept-only) based on Akaike's information criterion corrected for small samples (AIC_c). We derived model weights ($wAIC_c$) from the AIC_c difference between models (ΔAIC_c). The evidence ratio (*ER*) is the ratio of these weights, showing that the SAR model is 50.4 times more likely than the null. *k* = number of estimated parameters; R_m = marginal R^2 as a measure of goodness of fit.

model	***k***	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**R_m**	**evidence ratio (ER)**
SAR	2	-6.11	-	0.98	42.1	50.4
intercept-only	1	1.72	7.84	0.19	-	

The low alpha diversity (local diversity) and high beta diversity (change in diversity over space) demonstrated within Ediacaran communities (compared to modern communities) might be attributable to the varied periods of time between burial events. The high beta diversity in particular, is potentially reflective of highly variable TOS maturity and generic diversity across beds (Droser *et al*. 2019; Finnegan *et al*. In press), and could cause the plotted fossil bed SAR variability seen here.

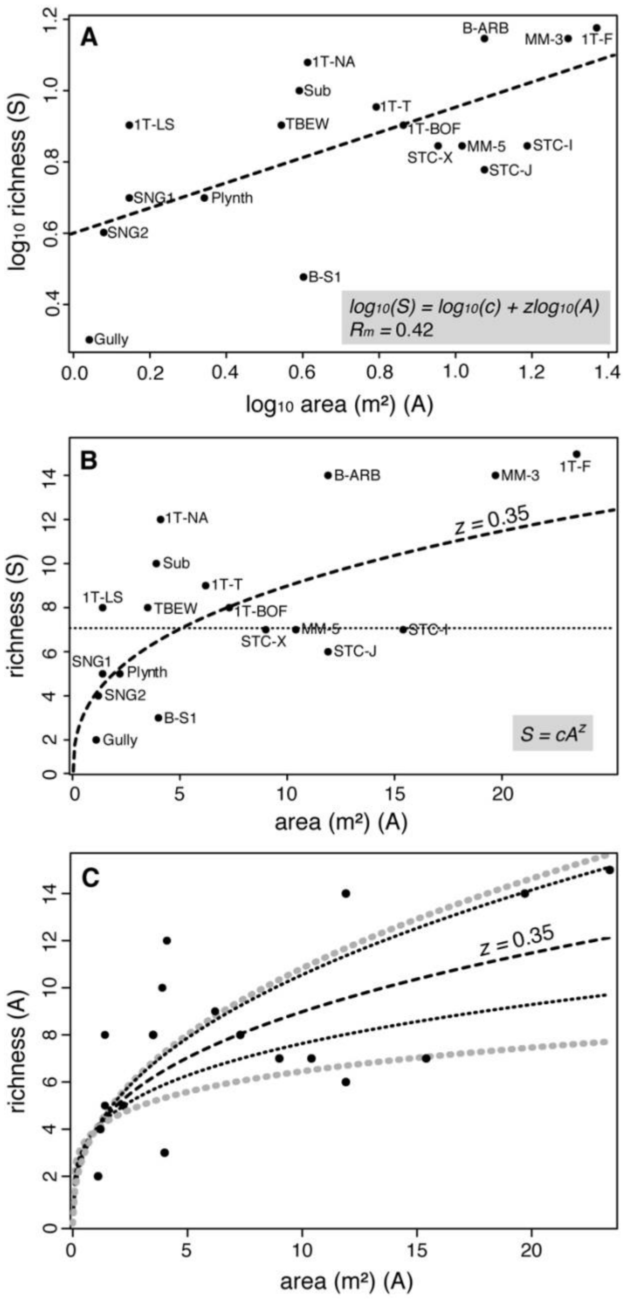

Figure 2. Species-area relationship (SAR) analyses of the fossil beds and their comparison with the metadata analysis from Triantis *et al*. (2012). **(A)** Regression plot of $\log_{10}$ area (A, in m^2) vs $\log_{10}$ richness (S) shows a strong, positive relationship (evidence ratio = 50.4; $R^2 = 0.42$). **(B)** Plot of area (m^2) vs richness follows the power-law species-area relationship of $S = cA^z$, where S increases as a power-law function ($\hat{z}$ = 0.35, black dashed line) of A. The horizontal black dotted line represents the null hypothesis of no relationship between species-area and richness. **(C)** The same plot as (B), except here we Gaussian-resampled the Ediacaran z exponent (SD = 0.11) 10,000 times and plotted the lower and upper quartiles (black dotted lines) of the fitted relationship. For comparison, we Gaussian-resampled 10,000 times the mean and SD of z from Triantis *et al*. (2012) for living communities and plotted their lower and upper quartiles (grey dotted lines).

6.6 Discussion and conclusion

Our analyses demonstrate that the ecological assembly rules estimated using the phenomenological species-area relationship for ancient Ediacaran fossil communities largely follow expectations derived from living communities. This is both surprising and unprecedented, particularly because the Ediacaran fossil communities from the Flinders Ranges are some of the earliest examples of complex multicellular life on Earth, they have low overall taxonomic richness, and there is as yet no documented evidence that predation was regulating these communities.

The potential biotic and abiotic parameters shaping species-area relationships is a hot topic among ecologists. Predation (Ryberg & Chase 2007), dispersal ability, and competition (Shurin & Alan 2001) have all been found to influence this fundamental ecological law. Studies have shown that the influence of predation within an ecosystem depends to some degree on environmental productivity (Proulx & Mazumder 1998; Chase *et al*. 2002; Kneitel & Miller 2003; Östman *et al*. 2006; Ryberg & Chase 2007). Therefore, in order to infer the impacts of predation or lack thereof on Ediacaran communities, we first need to establish whether these ancient communities were high- or low-productivity environments. A recent study by Pehr *et al*. (2018) investigating the lipid biomarker and stable isotopes of Ediacaran sediments (from communities in Eastern Europe) suggest that whilst Ediacaran environments were oxic and dissolved organic matter was high, the shallow Ediacaran seas of the Baltica were technically oligotrophic (non-productive). In high-productivity environments, predation regulates the food web such that dominant species do not establish, thus increasing species diversity relative to area (i.e., increasing *z*) (Chase *et al*. 2002). On the other hand, predation can have the opposite effect in low-productivity environments by increasing the likelihood of prey extinction and reducing species richness (Chase *et al*. 2002). Therefore, with a lack of apparent predation in a low-productivity environment, we could conceivably expect Ediacaran communities to demonstrate a higher species accumulation rate with area (higher *z*), than if predation was present. If the Flinders

Ranges material is similar to Eastern Europe, then consistent with this we might infer that both regions shared low-productivity environments. Thus while this makes for an interesting comparison, without the same analysis of Ediacaran sediments from the Flinders Ranges, i.e. analyses of lipid biomarkers and stable isotopes from drill cores, the productivity of the Ediacaran in the Flinders Ranges remains uncertain.

Ediacaran fossil communities demonstrate low alpha diversity, but high beta diversity, compared to Phanerozoic fossil assemblages and living communities (Finnegan *et al*. In press), possibly resulting from low motility and larval dispersal and a lack of disturbance by bioturbators in the former (Finnegan *et al*. In press). Furthermore, the inflicted disturbance of repeated sediment deposition over Ediacaran communities would have facilitated a lower alpha diversity, by placing time constraints on community maturation (Droser *et al*. 2019), whilst increasing beta diversity (Hawkins *et al*. 2014).

We have assumed that different Ediacaran species belonging to the same genus share a similar ecological niche. The iconic Ediacaran genus *Dickinsonia*, for example, contains five recognised species (Gehling *et al*. 2005), all of which are low-lying, epibenthic, and leave characteristic trace fossils potentially indicating a shared feeding strategy. Furthermore, the ecological niche of an organism is influenced by its environment/habitat, and we know that genus-wide limitations are inferred by specific submarine environments (Gehling & Droser 2013). Thus, while morphologically distinct Ediacaran specimens might be identified as different species, their shared gross morphological characters, 'ecospace' occupancy (Bambach *et al*. 2007), and feeding strategies could suggest genus-specific ecological niches. In the meta-data analysis by Triantis *et al*. (2012), they utilise datasets that are specific to species-level only. It is conceivable that we obtained a similar z value because while living communities are more species-rich, Ediacaran organisms may have maintained a similar diversity at the genus level only. Ediacaran communities demonstrate low alpha-diversity, but high beta-diversity, potentially reflective of high niche specialization. Thus, the fact that we are getting z exponents consistent with living communities, might arise because of a trade-off between these two components.

Interestingly, our $\hat{z}$ exponent of 0.35 more closely resembles that estimated from invertebrates and plants ($z = 0.323 \pm 0.014$ and $z = 0.355 \pm 0.150$, respectively) living within continental shelf and oceanic island environments ($z = 0.300 \pm 0.008$ and $z = 0.379 \pm 0.017$, respectively), and is larger than for communities containing vertebrates living within inland environments ($z = 0.287 \pm 0.010$ and $z = 0.285 \pm 0.020$, respectively; Triantis *et al*. 2012). This is consistent with the invertebrate affinities of some described Ediacaran forms (Fedonkin & Waggoner 1997; Gehling 1988; Droser & Gehling 2008), while others are more mysterious or of possible algal affinity (Xiao *et al*. 2013).

Our findings raise questions about why Ediacaran communities adhered to the same species-area relationship as modern communities, which encompass apparently more complex ecologies. For instance, how can the apparent lack of an important ecological function such as predation not influence its species-area relationship? The relationship between predation and species richness is complex (Chase *et al*. 2002; Ryberg & Chase 2007), with interspecific competition possibly also being a strong driver of species-richness patterns (Chase *et al*. 2002). Competition is an important driver of diversification, niche partitioning, and reproduction among Ediacaran assemblages globally (Clapham & Narbonne 2002; Bambach *et al.* 2007; Droser & Gehling 2008; Mitchell *et al*. 2015), and has been suggested as a stronger driver of diversification within Ediacaran communities than Phanerozoic and living communities (Finnegan *et al*. In press).

Here, we have demonstrated that certain fundamental ecological rules that apply to living communities are also manifested in ancient Ediacaran fossil communities. This is important because it means from the first appearance of multicellular communities on Earth through to the complex and highly diverse communities that exist today, fundamental ecological rules do not appear to have changed much over more than a half a billion years.

6.7 Acknowledgements

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6.9 Supplementary Information

Supplementary Table 1. Raw data table used for the SAR analyses. The table contains which sedimentary facies each fossil bed is from, the name of each fossil bed, the total number of individual specimens and diversity on each bed, as well as the total measured area of each bed (m^2).

Facies	Bed name	Number of individuals	Diversity	Area (m^2)
Oscillation-Rippled Sandstone	**MM-3**	307	14	19.7
	MM-5	34	7	10.4
	B-S1	23	3	4
	B-ARB	220	14	11.9
	STC-I	90	7	15.4
	STC-J	54	6	11.9
	STC-X	40	7	9
	1T-BOF	306	8	7.3
	1T-F	208	15	23.4
	1T-LS	51	8	1.4
	1T-T	252	9	6.2
	1T-NA	73	12	4.1
	Gully	14	2	1.1
	Plinth	73	5	2.2
	SNG1	121	5	1.4
	SNG2	120	4	1.2
Planar-Laminated and Rip-Up Sandstone	**Sub**	373	10	3.9
	TBEW	56	8	3.5

Chapter 7

7.1 Summary, implications and future work

The Ediacaran Period was monumental in the evolution of life on Earth, for it was then that some of the first complex, multicellular life on Earth was preserved in exquisite detail within expanses of fossilised seafloor. But there is still much uncertainty about the biological affinities of these enigmatic organisms. In this thesis, I set out to unveil some biologically significant attributes of the abundant Ediacaran fossils in my 'backyard' — the Flinders Ranges of South Australia. By observing fossil surfaces in detail, and applying statistically robust techniques on the spatial associations and orientations of specimens, I feel that the contributing authors and myself have achieved this.

I focussed much of the thesis on the shield-shaped fossil *Parvancorina*, particularly specimens from fossil surfaces excavated from Ediacara Conservation Park where they are locally abundant (Chapter 2). The high resolution of the fossil beds from there were essential for resolving some of the smallest specimens of *Parvancorina* found anywhere in the world, and provided new insights into the growth, development, and autecology of this ancient organism (Chapter 3). Spatial analyses of *Parvancorina* in Chapter 2 showed significant ecological information about the genus, which supports the need for continued research in this field. Further investigation into different spatial, analytical and interpretative methods could reveal more information about the genus. More specifically, analyses of size-distance patterns could reveal patterns of aggregated or stepped size classes, and could provide inferences about the reproductive method employed by *Parvancorina*.

From Ediacara Conservation Park, I also had the opportunity to discover and name one new taxon, and jointly discover another (Chapter 2) — the first of which I was fortunate enough to describe in this thesis (Chapter 5). The discovery of the possible stem-group mollusc *Velocephalina* *greenwoodensis* from Ediacaran-aged deposits not long after detailed observations of these fossil surfaces suggests that other novel forms could be discovered from there with more investigation. Further investigation into the morphology of the second undescribed genus (Form 2), mentioned in Figure 3 of Chapter 2, is necessary to provide more robust evidence of its potential phylogenetic affinities. Future studies of Form 2 would benefit from the analysis of numerous specimens across a variety of sizes, and in-depth analysis of their growth trajectories and corresponding number of segments. Such a paper is currently in the works by J. Gehling, C. Peddie and me, and is expected to be published sometime this year.

I must emphasise the importance of continuing palaeoecological research at Ediacara Conservation Park. The low-lying hills, sub-horizontal bedding surfaces, ease of access, and remarkable preservation of the fossil surfaces make it an ideal site for future discoveries of global importance and interest. Diminutive fossils of superb detail that are as yet not found anywhere else in the Flinders Ranges abound there (Glaessner & Wade 1971, Chapter 2). However, many of these both described and undescribed forms have received little research attention.

Investigating inter-taxa associations could reveal important information regarding the ecology of the Ediacara biota; however, this would be challenging due to the limited number of available fragment sizes of fossil sea floor. Therefore, to increase our understanding of phylogenetic affinities and ecology of the Ediacaran biota, future analyses need extensive field work, with a focus on the discovery, preservation and replication of larger areas of fossil seafloor. Furthermore, research at Ediacara Conservation Park has been somewhat limited relative to Nilpena since the initial discovery of the first Australian Ediacaran fossil here in 1946 (Sprigg 1947). To increase the research potential at Ediacara Conservation Park, opportunities should be made available for more PhD and postdoctoral students (both domestic and international) to study this remarkable site.

While a large, contiguous fossil surface has been excavated from Ediacara Conservation Park (NECP Bed-1, Chapters 2 — 4), many smaller pieces of fossil float material remain that do not directly attach to this bed. However, shared sedimentary and community characteristics imply that these float pieces originated from an extension of NECP Bed-1, or at least directly from a bed above or below it. Since its initial discovery, excavation and analysis, we have returned to the original excavation site of NECP Bed-1 and have excavated another ~ 3 m^2 of fossil seafloor. However, due to a lack of exposure and subsequent weathering of this new addition, extensive, fine-sediment 'shim' concreted on the surface remained, preventing immediate analysis and subsequent inclusion in my thesis. Since then, the volunteers at the South Australian Museum, most notably M. Ellis, have spent many hours carefully removing the surficial sand and silt to reveal the fossil community in pristine condition. NECP Bed-1 now comprises > 5 m^2 of a dense Ediacaran community, of which juvenile *Parvancorina* specimens are the most prevalent form. While I did not report this additional fossil area of NECP Bed-1 in this thesis, I anticipate that future work will investigate the ecology of this now-larger community on NECP Bed-1.

Access to the large collection of *Parvancorina* specimens in storage at the South Australian Museum, as well as a large population of specimens from 'Parv Bed' at Nilpena, provided ample data for the in-depth analyses of *Parvancorina* shape using morphometrics. In Chapter 4, I showed that *Parvancorina* was a highly flexible organism and most probably had the ability to alter its body proportions in response to environmental cues. Importantly, this contradicts previous interpretations of *Parvancorina* as a sclerotised stem-group arthropod (Zhang *et al*. 2003; Lin *et al*. 2006). My work also emphasises the use of morphometrics as a valuable tool in assessing

Ediacaran fossils, specifically where their dorsal exposure and near 2-dimensional preservation allows for consistently identifiable traits to be analysed. Future shape analysis of other Ediacaran fossils should follow, as they could potentially reveal morphologically and developmentally important insights into these first metazoan taxa.

To gain a more complete understanding of early life, we should consider that the precursors of characters that we now use to define specific phyla had an evolutionary history of change themselves. For example, a key trait that largely defines the phylum Arthropoda is the presence of a mineralised exoskeleton. The strict definition of an arthropod requires the presence of an exoskeleton, and in turn, jointed appendages (among other characters) to be present; however, palaeontologists often do not question what the precursors of arthropods might have looked like. Instead, we acknowledge that there is no evidence of invertebrates with exoskeletons or jointed appendages present before the Cambrian, and so we conclude that true arthropods must have evolved in the comparatively short, 20 million-year interlude between Ediacaran and Cambrian deposits. Would not a more parsimonious conclusion be that the precursors to arthropods were soft-bodied counterparts? *Parvancorina* has the trilobed body plan of a basal arthropod (Zhang *et al*. 2003; Lin *et al*. 2006), yet it is highly flexible, suggesting that it lacked a mineralised exoskeleton. Theoretically, future work using systematic and molecular methods targeting the Arthropod genes that drive exoskeleton mineralisation *versus* those that code for the trilobed body plan, could conceivably be used to solve the question of which trait is more evolutionarily basal.

In Chapter 6, I contributed to the collective knowledge of Ediacaran ecosystems by demonstrating that even the earliest communities adhered to the same fundamental community-assembly laws that modern communities do. While impending time restrictions prohibited additional data collection, further development of this chapter with added community datasets from Ediacara Conservation Park, Flinders Ranges localities such as Crisp Gorge (Reid *et al*. 2017), and other Ediacaran sites such as the Avalon (Newfoundland, Canada) and the White Sea (Russia), would generate a more complete and comprehensive dataset to test the generalisability of the community-assembly rules to which the Nilpena sites appear to adhere. Additionally, continued and future efforts to excavate larger surface areas of contiguous seafloor would be beneficial for more in-depth analyses of Ediacaran community ecology. Larger habitats would allow the efficient use of quadrat-based sampling methods, which could provide information regarding species-specific behaviour, dispersal ability, reproduction, as well as intra- and inter-species interactions. Importantly, this method will be most effective if applied to larger surface areas, because local Ediacaran diversity is comparably low relative to Phanerozoic and modern diversity (Finnegan *et al.* In press).

While I based my thesis largely on physical observations and measurements of Ediacaran fossils, it is likely that fascinating ecological discoveries will be made in the near future through the application of scanning technology to 3-dimensional models. For instance, recent work by Rahman *et al*. (2015) applied computational fluid dynamics over a scanned 3-dimensional model of the radially symmetrical Ediacaran genus *Tribrachidium*. Their results were remarkable, and showed that the structured, triradial-surface topography of the organism would have slowed benthic currents, allowing suspended particles to precipitate over the organism — thus inferring that it was a suspension-feeder. Further, Darroch *et al*. (2017) also used computational fluid dynamics over three idealised models of *Parvancorina* to assess the relationship between its shape and the flow of benthic currents. From their results, they ruled out osmotrophy as a potential feeding method, favouring suspension-feeding or detrivory instead, and also showed that the ability to orient/move would have been highly beneficial for *Parvancorina* to minimise the amount of drag exerted by benthic currents. These results agreed with the selective orientation of *Parvancorina* with benthic currents as demonstrated by *Paterson et al*. (2016), and I further demonstrated in Chapters 3 and 4 that this orientation taxis was also related to morphological change with growth.

It would be particularly interesting to apply computational-fluid dynamics to whole Ediacaran community samples. For instance, laser-scanning technology could be used to generate 3-dimensional models of entire Ediacaran seafloor communities. Computational fluid dynamics applied over entire surfaces could reveal patterns of water-flow over the seafloor topography. Natural undulations in the seafloor, the locations of specific taxa relative to others (in particular, tall and frondose forms such as *Charniodiscus*; see Fig. 2 in Chapter 1), and the varied textured organic surfaces potentially influenced the patterns of benthic currents. Computer-generated 3-dimensional models of entire Ediacaran communities would therefore allow us to investigate the complex relationships between the locations of organisms on the seafloor, the effects their unique shapes have on fluid flow, whether they sit within toughs or crests, and aggregation patterns on fluid flow. In Chapter 3, I showed that juvenile *Parvancorina* from Ediacara Conservation Park were spatially aggregated on the Ediacaran seafloor. These aggregations would serve as prime examples on which to apply computational fluid dynamics to investigate fluid-flow trends over grouped individuals.

7.2 Conclusion

The Ediacara biota represent some of the earliest examples of complex animal life on Earth, and as such, their evolutionary importance is unquestionable. The study of Ediacaran fossil beds from the Flinders Ranges of South Australia has revealed specimens of major biological and ecological importance for our understanding of early life on Earth. In particular, the exquisitely preserved fossil communities at Ediacara Conservation Park have been investigated in a new light, exposing newly identified forms and described genera. My observations and analyses of the enigmatic Ediacaran fossil *Parvancorina* have revealed behavioural responses to stimuli, developmental patterns, and morphological shape-changing capacity within the genus. Furthermore, I have demonstrated that ecological assembly rules that govern modern communities also applied about half a billion years ago to samples of some of the first communities on Earth. While there is still much work to be done in deciphering the enigmatic ecologies and biological affinities of Ediacaran fossils, the future looks bright with the rapid advancement and use of digital technologies as investigative tools. Determining the biological affinities of organisms that existed around half a billion years ago and their evolutionary characteristics could assist in understanding the nuances of the evolution of all animal life. Furthermore, this knowledge of environmental adaptation and evolution on Earth could also help us envisage the plausible evolution of life on other planets (Cady & Noffke 2009).

7.3 References

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