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Phyllozoon and *Aulozoon*: key components of a novel Ediacaran death assemblage in Bathtub Gorge, Heysen Range, South Australia

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Abstract

The recognition of fossiliferous horizons both below and above the classical Ediacara levels of the Flinders Ranges, South Australia, significantly expands the potential of this candidate World Heritage succession. Here we document a small window into the biology and taphonomy of the late Ediacaran seafloor within the new Nilpena Sandstone Member of the Rawnsley Quartzite in Bathtub Gorge, northern Heysen Range. A 1 m^2 slab extracted from the gorge, now on permanent display at the South Australian Museum, has a death assemblage dominated by the erniettomorph *Phyllozoon hanseni* Jenkins and Gehling 1978 and a newly named macroscopic tubular body fossil – *Aulozoon soliorum* gen. et sp. nov. – on its fine sandstone bed sole. The orientations and juxtaposition of these taxa suggest overprinting of an *in situ* benthic *Phyllozoon* community by sand-filled tubes of *Aulozoon* carried in by a storm wave-base surge. *Phyllozoon hanseni* is a widespread species that is restricted to the Nilpena Sandstone Member of the Rawnsley Quartzite, whereas *Dickinsonia costata* ranges from the underlying Ediacara Sandstone Member into the Nilpena Sandstone Member. Fundamental differences in the ways these two vendobiont taxa are constructed and preserved may provide insights into their biology and phylogenetic affinities. In the Nilpena Sandstone Member, *D. costata* is joined by *Dickinsonia rex* Jenkins 1992, which appears to be confined to the member, and is here re-described to clarify its taxonomic status and stratigraphic distribution.

1. Introduction

The most distinctive and most commonly preserved soft-bodied Ediacaran taxa from the Flinders Ranges of South Australia are, in order of frequency, *Aspidella* Billings, 1872, *Dickinsonia* Sprigg, 1947, *Funisia* Droser & Gehling, 2008 and *Phyllozoon* Jenkins & Gehling, 1978 (Droser *et al.* 2006; Evans *et al.* 2016). These genera tend to be found in large numbers on particular horizons, often to the near exclusion of other forms. Here we describe a new occurrence of this type, an event bed from Bathtub Gorge, Heysen Range, central Finders Ranges (Figs 1–4), dominated by two distinctive taxa: *Phyllozoon hanseni* and a newly named tubular body fossil, *Aulozoon soliorum* gen. et sp. nov. We document this small window into the late Ediacaran seafloor, describe the morphology of the organisms, the taphonomy of the deposit and its stratigraphic context, and explore their roles in the microbial mat-dominated benthic community.

Most Ediacaran fossils are preserved on bed soles as either convex or concave moulds, but not normally as both. For example, discoidal form taxa such as *Aspidella* and *Cyclomedusa* Sprigg, 1949 are almost invariably preserved in convex hyporelief while more resilient, apparently tissue-grade forms such as *Dickinsonia* are preserved in shallow, concave hyporelief (Wade, 1968; Gehling, 1999). One of the two taxa dealt with here, *Phyllozoon hanseni*, is always preserved in convex relief on bed bases, is nearly always found in side-by-side arrays with other members of its cohort (Figs 5–8; online Supplementary Fig. S4, available at http://journals.cambridge.org/geo), and frequently overlies or underlies other taxa. In contrast, *Dickinsonia* is invariably preserved in concave hyporelief and is almost always well separated from other members of its species or other soft-bodied taxa. The exception that proves the rule are the convex hyporelief 'footprints' of *Dickinsonia* that are commonly considered to be resting traces left by mobile animals (Gehling *et al.* 2005; Evans *et al.* 2019). These and related matters are the subject of this article.

2. Stratigraphy and methods

In the Heysen Range, the late Ediacaran Pound Subgroup (there, *c.* 770 m thick) is composed of the red Bonney Sandstone and overlying white Rawnsley Quartzite (Figs 1, 2). Ediacaran fossils
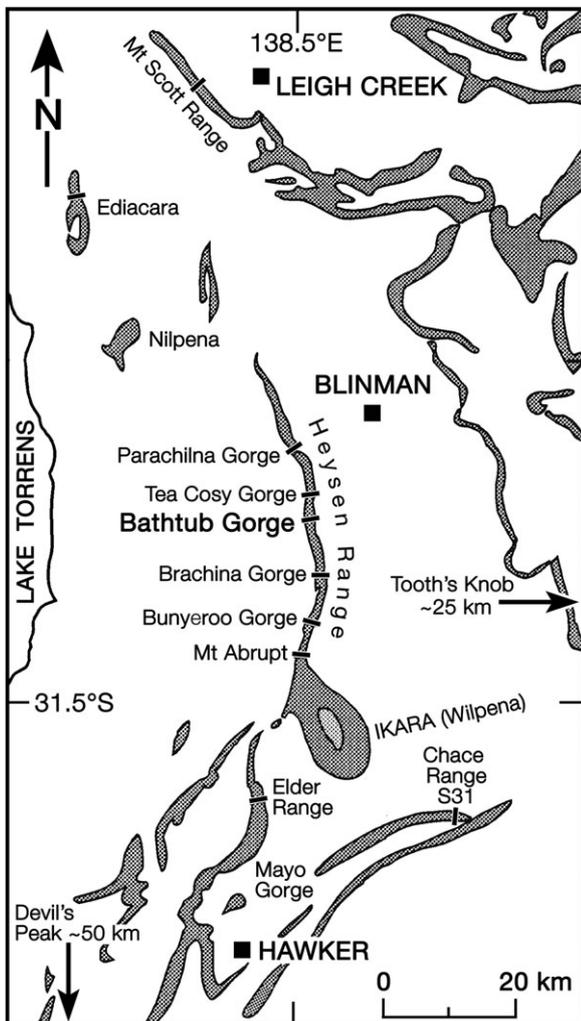
Fig. 1. Locality map for occurrences reported in the text. Grey shaded areas represent outcrops of the Pound Subgroup (Figs 2, 3). Tooth's Knob is *c.* 25 km to the east of the right edge of the map, near Reaphook Hill; The Devil's Peak, type locality for *Phyllozoon hanseni*, is *c.* 50 km south of the bottom edge of the map.
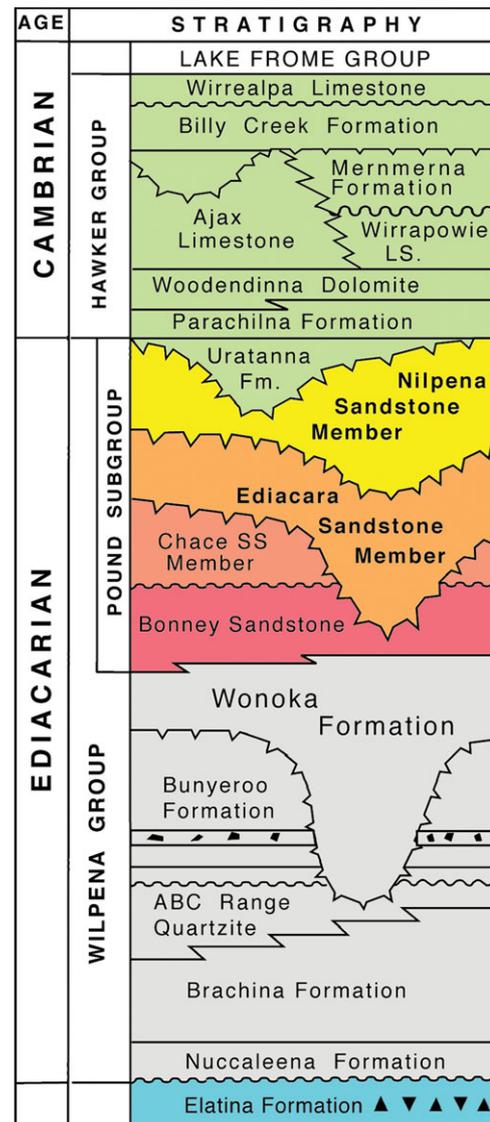

Fig. 2. Lithostratigraphy of the Ediacaran and lower Cambrian strata of the central Flinders Ranges, South Australia. The Ediacaran–Cambrian boundary is thought to coincide with the erosional surface at the base of the Uratanna Formation. The Uratanna Formation is missing from the section in Bathtub Gorge, Heysen Range (Fig. 3).

first appear in the Ediacara Sandstone Member of the Rawnsley Quartzite, which cuts disconformably down through the underlying Chace Sandstone Member into the Bonney Sandstone. However, the recent discovery of an erosional sequence boundary within the Ediacara Member in the Nilpena precinct of the Ediacara Conservation Park (Coutts *et al.* 2016) has led to the separation of a new uppermost Nilpena Sandstone Member of the Rawnsley Quartzite (Figs 2, 3; Gehling *et al.* 2019). The fossiliferous facies of the Nilpena Sandstone Member also form the uppermost sedimentary cycle of Rawnsley Bluff, the SE end of Ikara (Wilpena Pound), and in the contiguous Heysen Range they occur from *c.* 1 km south of Bunyeroo George northwards through Brachina, Bathtub and Tea Cosy gorges (Fig. 1).

Richly fossiliferous horizons in the basal part of the Nilpena Sandstone Member are well exposed in Bathtub Gorge, which is a deep incision through the Heysen Range north of Ikara (Fig. 1). There, individual fossil horizons were traced over a strike distance of *c.* 300 m and logged into sections measured through a shallowing-upwards cycle, which begins near the top of the Ediacara Sandstone Member and ends in the lower part of the Nilpena Sandstone Member (Fig. 3). These three local stratigraphic

sections, measured to decimetric accuracy, were keyed into a more general section through the Pound Subgroup in Bathtub Gorge (left column of Fig. 3). *Phyllozoon hanseni* and *Dickinsonia rex* Jenkins, 1992 are exclusive to the Nilpena Sandstone Member in both Bathtub Gorge and at Nilpena (Gehling *et al.* 2019). The holotype of *D. rex* is from approximately the same level in Brachina Gorge (Wade, 1972; Jenkins, 1992) and another specimen of *D. rex* from this interval, originally *c.* 1 m in length (Runnegar & Fedonkin, 1992, fig. 7.5.7D), was partially extracted, cast and replaced in Brachina Gorge (online Supplementary Fig. S5, available at http://journals.cambridge.org/geo). The only other taxon from Bathtub Gorge that appears to be restricted to the Nilpena Sandstone Member is *Palaeophragmodictya reticulata* Gehling & Rigby (1996), a putative glass sponge that occurs at the 4.5 m level in section 3 of Fig. 3. Elsewhere (Nilpena, Chace Range, The Devil's Peak; Fig. 1), *Eoandromeda octobrachiata* Feng *et al.* 2008, *Arkarua adami* Gehling, 1987, *Inaria karli* Gehling, 1988 and
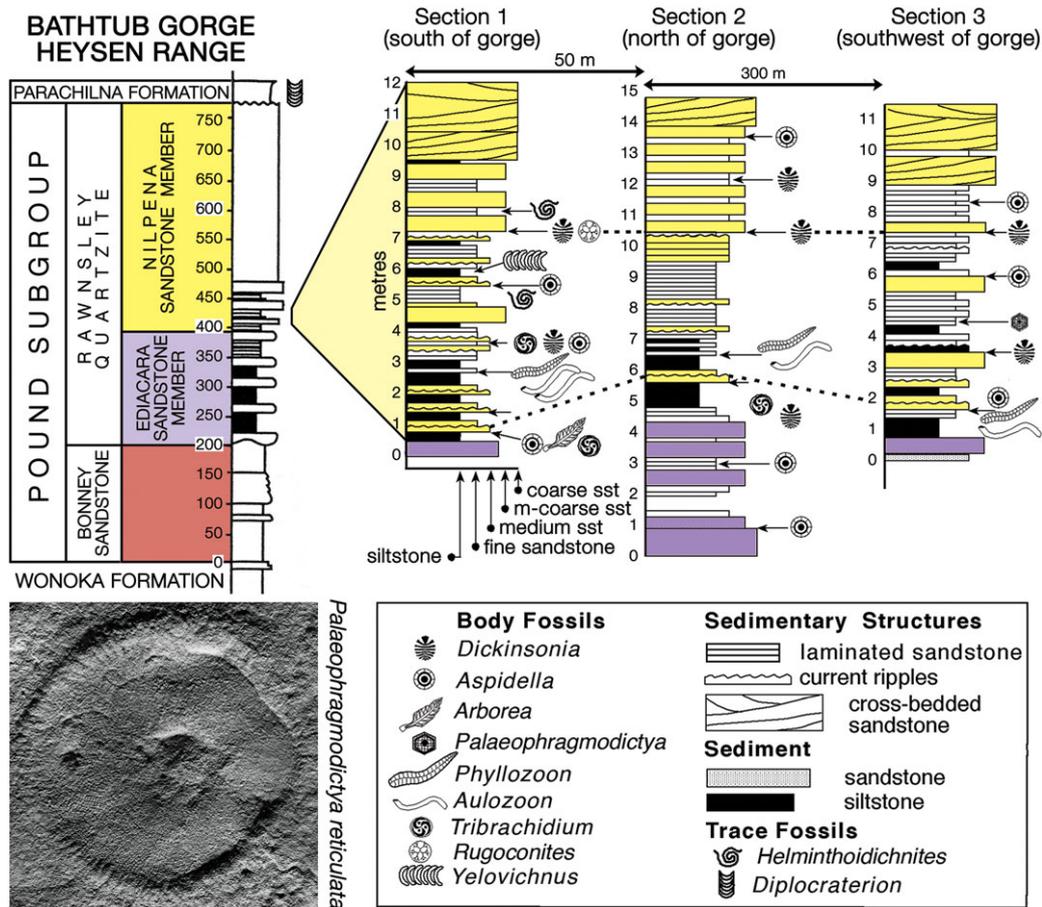
Fig. 3. Stratigraphy of the Pound Subgroup in Bathtub Gorge, Heysen Range, *c.* 30 km north of Ikara (Wilpena Pound), South Australia (Fig. 1); an outcrop view of section 1 is shown in Figure 4a. The assembled slab shown in Figure 5 is from the 6.7 m level of section 2 (Fig. 4b). The putative Ediacaran glass sponge *Palaeophragmodictya reticulata* (lower left, natural size) is found at the 4.5 m level in section 3 and *Dickinsonia rex* (online Supplementary Fig. S6b) at the 7.5 m level of section 1.
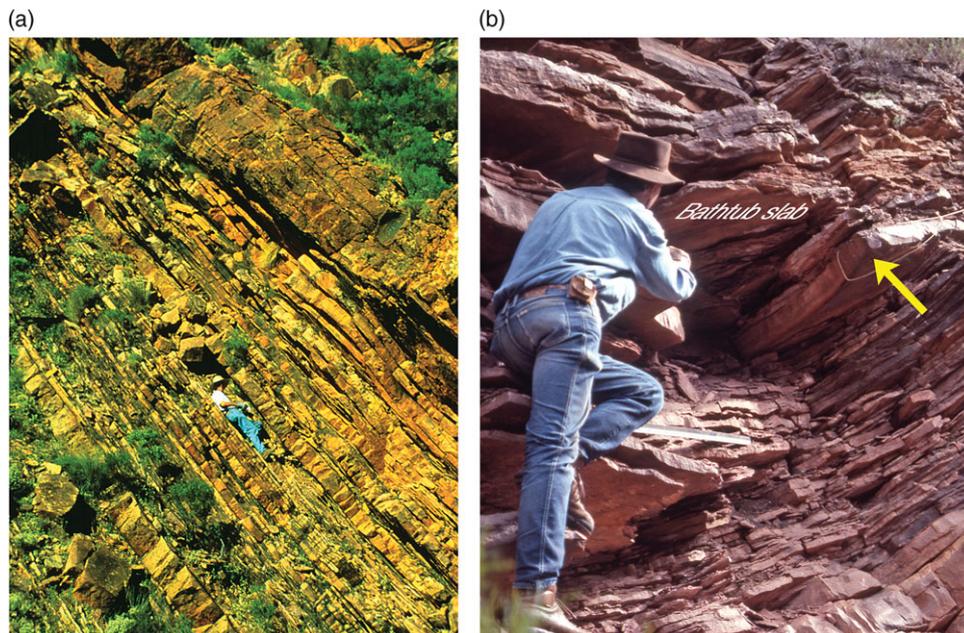
Fig. 4. Field photographs of the fossiliferous intervals, Bathtub Gorge. (a) Outcrop view of the lower part of the Nilpena Sandstone Member, Rawnsley Quartzite, in section 1 of Figure 3. The palaeontologist is making a latex cast of the 'beaver-tailed' specimen of *Dickinsonia rex* figured by Jenkins (1992, fig. 14; online Supplementary Fig. S6b), which is on the base of the bed above him (7.5 m level, section 1, Fig. 3). (b) Jim Gehling extracting the largest piece of the Bathtub slab in 1992. His right foot is on the thick bed just above 4 m in section 2, Figure 3; the arrow points to the bed at 6 m, and the Bathtub slab is *in situ* at 6.7 m.

Fig. 5. Map of the sole of the re-assembled slab, *c.* 1 m² in size, extracted from the 6.7 m level of section 2 (Fig. 3) in Bathtub Gorge, Heysen Range. The surface is dominated by specimens of *Phyllozoon hanseni* and *Aulozoon soliorum*, but there are al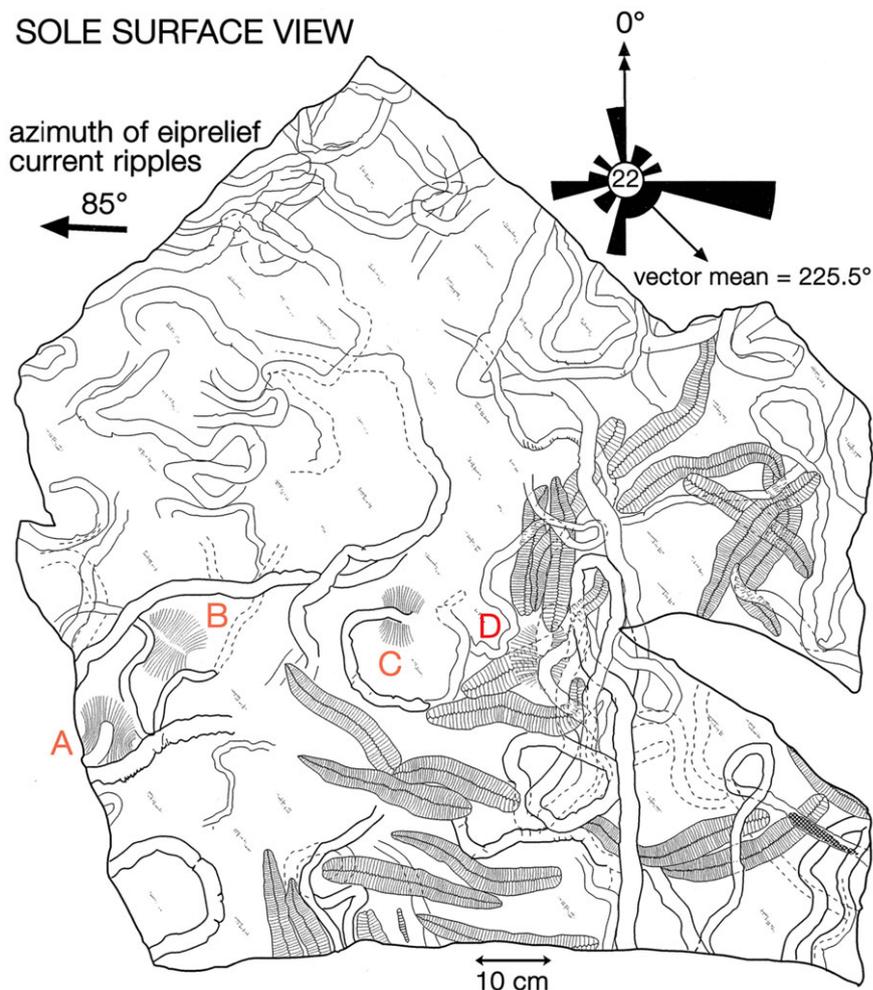so four 'footprints' of *Dickinsonia* cf. *costata* (A–D). The rose diagram shows the orientations of specimens of *Phyllozoon* with respect to the azimuth of crescentic ripple marks on the upper surface of the bed. In this view, east is left because the slab is inverted. This slab is on permanent display in the Ediacaran Gallery of the South Australian Museum.

Fig. 6. Base of sizeable slab from the Nilpena Sandstone Member, Rawnsley Quartzite, at the Nilpena precinct of the Ediacara Conservation Reserve illustrating how specimens of *Phyllozoon hanseni* are frequently found together, 'hugging' each other and even themselves. There are also several raised circular structures, poorly defined 'footprints' of *Dickinsonia costata* (black arrows) and an incomplete body fossil of *D. cotata* preserved in concave hyporelief (outlined; white arrow) on the *Phyllozoon* in the upper left corner of the slab. Note how adjacent modules of the *Phyllozoons* are juxtaposed at the sharp corners of the insides of tight turns. Boxed area is enlarged in Figure 7d; the large U-shaped specimen of *Phyllozoon* is SAM P57687.

an undescribed new species of *Tribrachidium* Glaessner in Glaessner & Daily, 1959 are also confined to the Nilpena Member (Gehling *et al.* 2019).

In Bathtub Gorge, as at Ediacara and Nilpena, the Nilpena Sandstone Member is disconformably overlain by the *Diplocraterion*-rich Parachilna Formation (Fig. 3; Jago *et al.* 2020), but in sections further north near Leigh Creek, the Uratanna Formation lies disconformably on the Pound Subgroup and is, in turn, conformably overlain by the Parachilna Formation (Fig. 2; Daily, 1973). Trace fossils and acritarchs suggest an early Cambrian (Terreneuvian) age for the Uratanna Formation (Daily, 1973; Jago *et al.* 2002; Betts *et al.* 2018).

Several fossiliferous horizons in Bathtub Gorge were traced out to link the three local measured sections; links were checked using bedding characteristics, and the consistency of preservation and composition of the fossils on each bed surface (Fig. 3). An oriented 1 m² sample was extracted and transported as three separate pieces from the 6.7 m horizon in section 2 (Figs 3, 4b; 31.245011° S, 138.538350° E). Many specimens of two common species – *Phyllozoon hanseni* and *Aulozoon soliorum* – are preserved as a complex tangle on this reconstructed slab, parts or all of which have been illustrated previously by Runnegar (1994), Seilacher *et al.* (2003, 2005), Gehling *et al.* (2005), Retallack (2007), Seilacher (2007) and Seilacher & Gishlick (2015). Prior to reassembly (Fig. 5, online Supplementary Fig. S7, available at http://journals.cambridge.org/geo), the three separate pieces, including the edges, were copied using
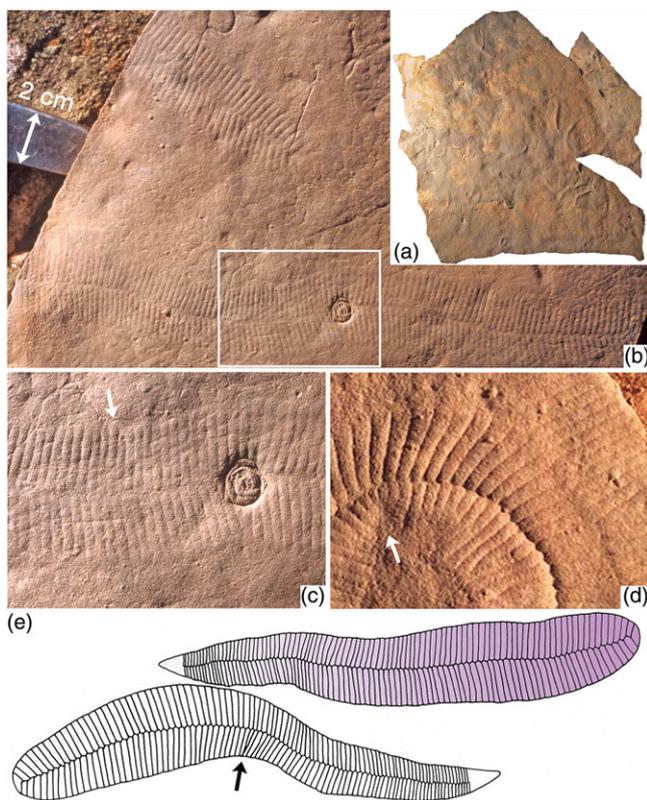
Fig. 7. Preservation and anatomy of *Phyllozoon hanseni*. (a) Image of the sole of the reassembled slab from Bathtub Gorge (Fig. 5), *c.* 1 m² in size. (b, c) Field photographs of a loose slab that was probably derived from the excavated horizon (6.7 m level, section 2, Fig. 3); boxed area in (b) enlarged in (c) to illustrate the rounded terminations of individual modules (arrow) and telescoping of modules at a link in the margin (up arrow); the round object is probably a frond holdfast (*Aspidella*). (d) Enlargement of boxed area of Figure 6 to show details of the frond margins, contact zones, axial seam and telescoped inner margin of tight turn (arrow); image is 5 cm wide. (e) Sketches based on two specimens of *P. hanseni* on the Bathtub slab (Fig. 5, bottom centre); growth proceeded from the rounded proximal end to the distal tapered end and is indicated by the gradient in the upper sketch; arrow points to telescoped modules on inner side of bend.
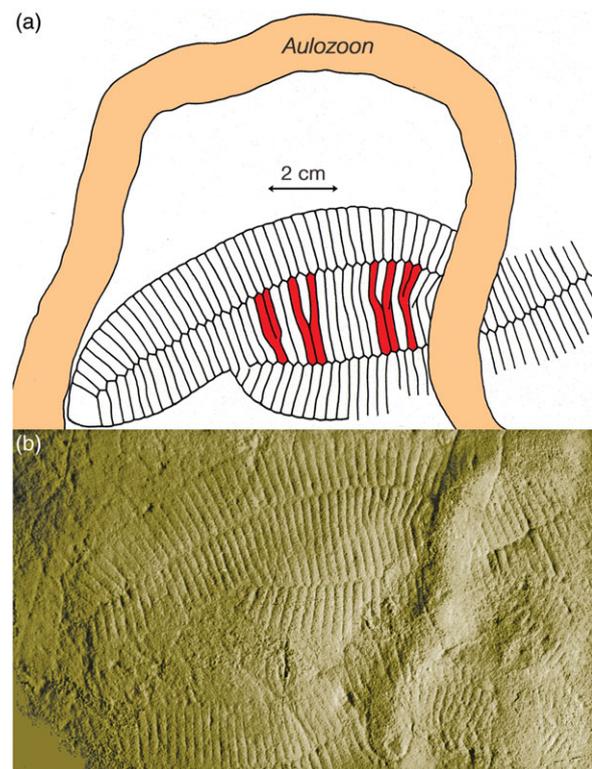

Fig. 8. (a) Sketch and (b) image of the lower surface of a loose slab from Bathtub Gorge that is almost certainly from the same bed as the large slab in Fig. 5. Two of the three individuals of *Phyllozoon hanseni* on this slab (SAM P35687-9) are partially overlapped, but the overlapped edges were not preserved. Small size differences between the tubular modules of the two individuals resulted in the centres of some modules of the upper individual overlying the seam between two modules of the lower individual. The spacing of these particular relationships is due to the vernier effect, highlighted by red shading. Slab previously illustrated by Gehling (1991, pl. 3, fig. 2) and Droser *et al.* (2005, fig. 5); see also Figure 9.

water-soluble latex plus medicinal bandages as a strengthening material. The resulting latex moulds were cast using uncoloured dental plaster. The edges and internal subdivision of fossils on the surfaces of these plaster casts were then traced with graphitic pencils, which provided sufficient contrast with the plaster to permit direct photocopying at half the original size. The reduced-scale photocopies were assembled into a mosaic, which was scanned electronically and used as the basis for the line drawing shown in Figure 5. The original photocopied mosaic has been rescanned for this work (online Supplementary Fig. S7); it represents raw data based directly on faithful copies of the fossils themselves. In contrast, the line drawing (Fig. 5) incorporates some degree of interpretation, albeit slight.

The azimuths of 22 specimens of the sword-fern-shaped frond of *Phyllozoon hanseni* on this slab were measured in 5 cm axial increments with respect to the average unidirectional transport direction indicated by asymmetric ripples on the upper surface of the slab and then averaged for each individual frond (Fig. 5). The cumulative widths of lateral modular elements were measured parallel to the axis on both the left and right sides of selected specimens and plotted to show the rate of growth (online Supplementary Fig. S1, available at http://journals.cambridge.org/geo). All other specimens used in this analysis were collected

from horizons that were traced to the three measured sections. Sawn and smoothed sections were cut of the *Phyllozoon* bed in order to study the texture of the sole surface and the sand fill of tubular fossils. Catalogued figured material is included in the palaeontological collection of the South Australian Museum with numbers prefixed SAM P; other illustrated material remains in the field.

3. Taphonomy of the *Phyllozoon* bed in Bathtub Gorge

3.a. Introduction

A small window to the sea floor is provided by the undersurface of the reassembled *c.* 1 m² slab (Figs 5, 7a; online Supplementary Figs S2, S7, available at http://journals.cambridge.org/geo), which was extracted from the north wall of Bathtub Gorge (6.7 m level of section 2; Figs 3, 4b) and is now part of the permanent display of Ediacaran fossils at the South Australian Museum. We use that surface and other pieces of the same bed found in place or as loose blocks in Bathtub Gorge to reconstruct the death assemblage captured by the deposition of this of 3–4-cm-thick event horizon. In addition to *Phyllozoon hanseni* and *Aulozoon soliorum*, which dominate the surface (Fig. 5), there are four indistinct impressions of sizeable individuals of *Dickinsonia* cf. *costata*, also preserved in convex hyporelief (Fig. 5, A–D). These are regarded as resting traces of the kind that elsewhere are commonly associated with overlapping 'footprints' made by individuals of *Yorgia waggoneri*

Table 1. History of interpretations of the biology and taphonomy of the Bathtub Gorge slab surface and the organisms that inhabited it. Az – *Aulozoon*; Pz – *Phyllozoon*; Dick – *Dickinsonia*; mat – microbial mat; – symbolizes adjacency and / represents an interface between overlying and underlying organisms

Reference	*Phyllozoon*	*Aulozoon*	*Dickinsonia*	Superposition
Glaessner, 1969		Trace fossil		Mat/Az
Jenkins & Gehling, 1978	Petalonamae			Pz/mat
Gehling, 1991	Vendozoa	Body fossil		Az/Pz/mat
Fedonkin & Runnegar, 1992		Body fossil		Az/mat
Runnegar, 1994		Body fossil		Pz–Az/mat
Seilacher *et al.* 2003	Vendobiont	Backstuffed burrow	Vendobiont	Dick/mat/Az
Seilacher *et al.* 2005	Vendobiont	Backstuffed burrow	Vendobiont	Dick/mat/Pz–Az
Retallack, 2007	Window lichen	Rhizome	Thallus/mushroom	Dick/mat/Pz/Az
Ivantsov, 2011	Trace fossil	Body fossil		Az/Pz/mat
Retallack, 2013	Window lichen	Rhizome	Thallus/mushroom	Dick/mat/Pz/Az
Retallack, 2016	Window lichen	Rhizome	Thallus/mushroom	Dick/mat/Pz/Az
Seilacher & Gishlick, 2015	Vendobiont	Backstuffed burrow		Mat/Pz/Az
This study	Erniettomorph	Body fossil	Trace fossil	Az/Pz–Dick/mat

Fig. 9. Holotype of *Aulozoon soliorum*, SAM P35690 (black arrows) and another partly superimposed unregistered specimen of *A. soliorum*, preserved in convex hyporelief, that ends in a rounded termination (white arrows); lower Nilpena Sandstone Member, Bathtub Gorge; see also Figure 8. Both ends of the unregistered *Aulozoon* are overprinted by *Phyllozoon*, whereas the holotype interrupts the two *Phylozoon* fronds where it crosses them. This is the kind of evidence that supports the 'winnowed and transported' hypothesis (Fig. 11a).
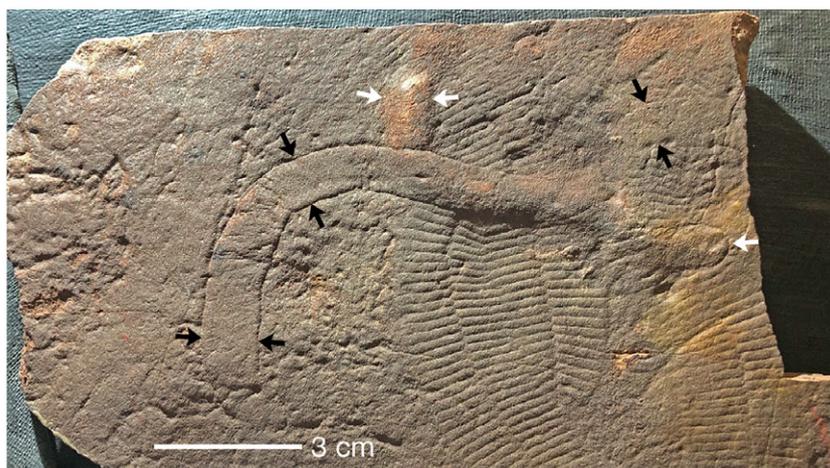
and *Dickinsonia costata* (Ivantsov & Malakhovskaya, 2002; Gehling *et al.* 2005; Ivantsov, 2011; Evans *et al.* 2019). One sizeable piece of sandstone, which was not *in situ* but is probably from the slab level, has crisp, fan-shaped arrays of paired scratch marks – *Kimberichnus teruzzii* Ivantsov, 2013 – partly overlapping fronds of *Phyllozoon hanseni* (online Supplementary Fig. S3a, available at http://journals.cambridge.org/geo).

In which order did these four unrelated species end up on this deeply subtidal matground? In order to answer this question it is necessary to derive the superpositional order from overlapping relationships as seen on the bed base (Figs 5, 8–10; online Supplementary Figs S2, S3), which is equivalent to looking upwards into the water column from beneath the sediment-water interface. In this view, structures in the foreground were there first but were cast by sand falling from the background. However, two or more taxa may have been superimposed and then amalgamated by compaction into a composite cast of the underlying bed top following the removal of all organic matter (Fig. 9; online Supplementary Fig. S3b–d). It may therefore be difficult to be certain of the original order of deposition. An additional complicating

factor is that understanding of the biology and preservation of the organisms has also evolved over several decades. In order to summarize these disparate biological and taphonomic alternatives, Table 1 gives a history of the various interpretations of the Bathtub slab surface and the organisms that are found on it; Figure 11 summarizes the three main taphonomic hypotheses: (a) *ex situ* death assemblage (Gehling *et al.* 2005); (b) *in situ* life assemblage (Seilacher *et al.* 2003, 2005; Retallack, 2007, 2016); or (c) *in situ* Phyllozoon, *ex situ* Aulozoon (this study).

3.b. Previous interpretations of the biostratinomy and taphonomy

Adolf Seilacher spent some time studying and sketching the first piece of the Bathtub slab, which was collected in 1991 (Runnegar, 1994; Seilacher *et al.* 2003, 2005; Seilacher, 2007; Seilacher & Gishlick, 2015). He interpreted the palaeoecology of the site in the following way: 'Uniformly sized vendobionts (*Phyllozoon*) were living below the mat and are therefore perfectly preserved in their original "hugging" positions. *Dickinsonia*,
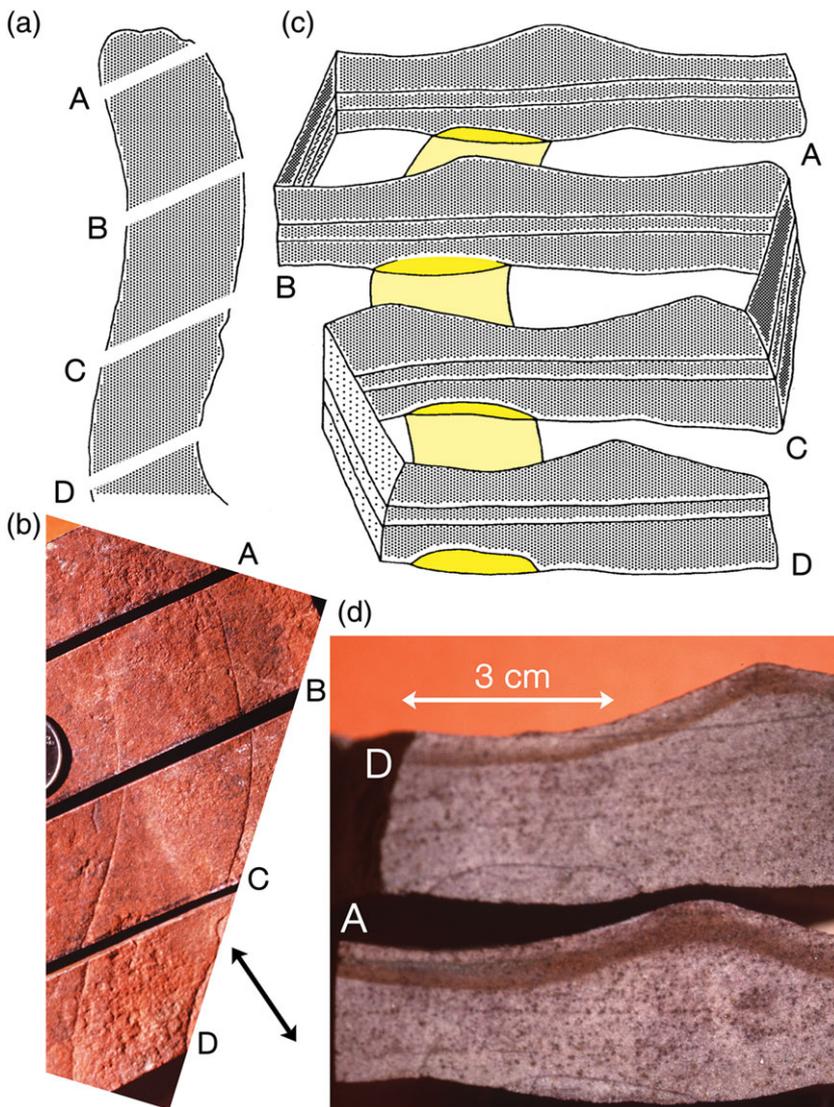
Fig. 10. Sketches (a, c) and images (b, d) of a paratype of *Aulozoon soliorum* (SAM P58399A-D), Ediacara Sandstone Member, Rawnsley Quartzite, Mount Scott Range, South Australia. Specimen (b), which was not *in situ*, has been sawn into four pieces to reveal cross-sections of the tube, A and D in (d), as shown diagrammatically in (a) and (c). Note ripple crests on top and base of bed in (b) and (d); black arrowed line indicates trend of ripple crest on bed sole.

in contrast, lived solitarily on top, where it could use its limited mobility . . . to digest new areas of the living mat. Accordingly, *Dickinsonia* specimens are preserved only as vague phantoms pressed through the mat by compaction. In the trace fossil interpretation, while bulldozing along the base of the biomat, the *Aulozoon* producer reacts upon collision with an undermat *Phyllozoon* in specific ways. If approaching it at a low angle, the animal contours the vendobiont and turns away, while collisions at larger angles are avoided by passing either above or below the *Phyllozoon*. In contrast, *Aulozoon* does not react to the *Dickinsonia* phantoms. All this speaks for a smothered matground, in which *Phyllozoon* grew below the biomat and *Dickinsonia* lived on top.' (Table 1; Fig. 11b; Seilacher *et al.* 2005, p. 329; Seilacher, 2007, p. 178). This view was reinforced prior to his death in 2014: 'Another member of this community, "Aulozoon" (invalid name) is here interpreted as the backstuffed burrow of a flatworm. As it moved under the mat for getting food and oxygen, it avoided the vendobionts by either turning away or passing underneath them.' (Seilacher & Gishlick, 2015, p. 142).

Greg Retallack (2007, 2016) came to a radically different interpretation. He agreed with Gehling *et al.* (2005) that *Aulozoon* was a body fossil rather than a trace fossil, but speculated that, because of an association of the ends of *Aulozoon* tubes with all four specimens of *Dickinsonia* of the Bathtub slab (Fig. 5, A–D), *Aulozoon* must be the vegetative mycelial rhizomorph of the thallus (mushroom), *Dickinsonia*. This was another in a long list of criteria for considering the classical Ediacaran assemblages to be terrestrial (e.g. Retallack, 2013).

Unsurprisingly, we reject Retallack's scenario for reasons discussed elsewhere (Xiao *et al.* 2013; Runnegar, 2021). Seilacher's idea that *Phyllozoon* was a benthic organism that lived below the mat is similar to our proposal that *Phyllozoon* was a prostrate inhabitant of the matground but, by analogy with other erniettomorphs that seem to have lived in the water column (Runnegar, 2021), we prefer the scenario of a mat top lifestyle (Table 1; Fig. 11c). Seilacher's undermat miner interpretation of *Aulozoon* is falsified by the geometry of the tubes, their lenticular cross-sections (Fig. 10) and the fact that they are in the event bed, not beneath the mat. The possibility suggested by Ivantsov (2011) that *Phyllozoon* is the resting trace of a proarticulate animal similar to *Dickinsonia* was based mainly on a reinterpretation of the holotype, which is not well preserved. Better material found subsequently (Fig. 6) makes this suggestion implausible.
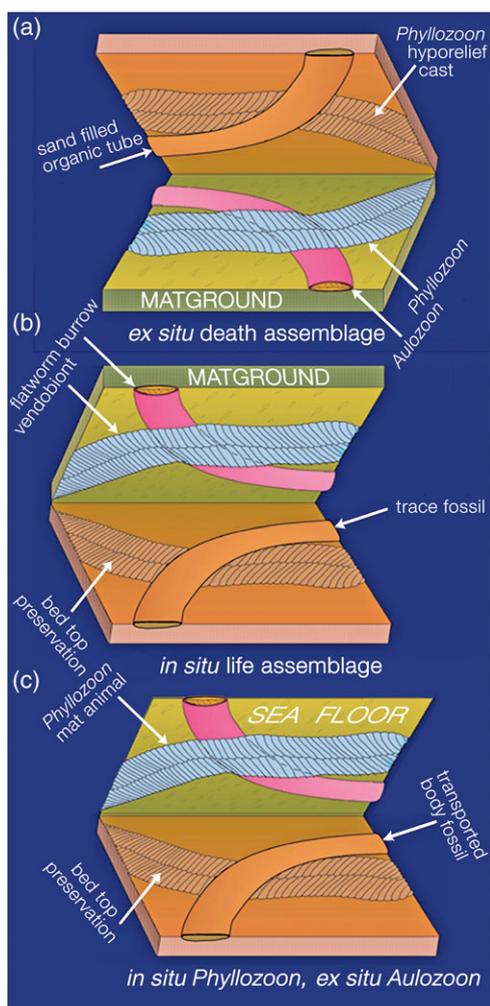
Fig. 11. Three hypotheses for the taphonomy of the assemblage on the Bathtub slab surface: (a) 'winnowed and transported assemblage' Gehling *et al.* (2005); (b) benthic community of mat-hugging photosynthetic vendobionts (*Phyllozoon*) and undermat flatworm bulldozers (*Aulozoon*), after Seilacher *et al.* (2003, 2005); and (c) our current hypothesis of *in situ* matground fronds (*Phyllozoon*) and sand-filled *Aulozoon* body fossil tubes, which were carried in by the storm surge that deposited the 3–4-cm-thick event bed.

3.c. Preservation of the fossils and biostratinomy

The two common body fossils – *Phyllozoon* and *Aulozoon* – seem to be tangled together as if transported and deposited by the storm surge itself (Gehling *et al.* 2005). However, this begs the question as to how incompletely sand-filled tubes (*Aulozoon*) and fluid- or tissue-filled fronds with a specific gravity of *c.* 1 (*Phyllozoon*) could be laid down together prior to burial by denser quartz sand. In addition, there is a notable paucity of overlap between adjacent individuals of *Phyllozoon*, and even *Phyllozoon* by *Aulozoon*, many of which 'hug' the outlines of the fronds (Figs 5, 6, 8; online Supplementary Fig. S4). We shall return to these matters, but first look at the preservation of this bed in more detail.

The smoothness of the bed sole, and its cementation with quartz and iron oxides, contrasts with the sugary, iron-oxide-poor surface of the underlying bed top. The parting medium was likely to have been the microbial mat that sealed the underlying sediment surface like cling film and allowed sand grains to settle and pack into the most compact arrangement possible. In contrast, the underlying bed top was formed during the waning current of a previous storm

surge, so the sand grains remained loosely stacked. All specimens of *Phyllozoon* are preserved in convex hyporelief, presumably cast from impressions of the frond in the mat substrate prior to collapse of the modules and the onset of decay. Numerous examples of convex parts and concave counterparts, without an intervening clay or silt lamina, have been found. *Phyllozoon* may either have been pressed into the mat and the underlying unconsolidated bed top by the weight of the 3–4 cm thick storm surge sand that buried it, or have grown in place and moulded the mat accordingly. Deflation of the tubular modules must have preceded the cementation of the sole of the overlying sand, which cast the whole collapsed organism and the surrounding mat interface. Specimens of *Phyllozoon* that cross one another are preserved as composite moulds displaying the intersecting rib patterns of each individual (Figs 5, 6). There is no evidence that any specimens of *Phyllozoon* were filled with sand prior to burial or that the tubular modules collapsed unevenly. Relatively few specimens are visible in their entirety because the tapering distal ends are made from modules having progressively smaller width and relief, which are therefore less amenable to preservation. Most fronds are either straight or, more often, gently curved on the bed surface (Figs 5, 8; online Supplementary Fig. S4), but tight curvature also occurs (Fig. 6). On the inside edges of curved specimens, modules concertina rather than cross (Figs 6, 7b–d), which shows that they were joined to one another and not pinnate like sword fern fronds. The quilted arrangement of the modules and their resultant hydrostatic properties seem to have given the organism a considerable degree of planar rigidity, as indicated by the lack of folded or torn specimens.

Some *Phyllozoon* fronds are found lying in apposition, such that the module boundaries appear to line up between adjacent individuals and may even seem to continue from one individual to another (Figs 6, 8). This apparent biological continuity is explained by partial overlap followed by amalgamation during compaction; the Y-shaped connections are explained by a vernier effect, whereby two abutted sets of parallel lines with different spacing, such as the groves between modules of differently sized individuals, correspond only at certain positions. With some amount of overlap between subparallel individuals at the time of burial, younger modules of smaller size in one individual may split to accommodate the less numerous modules of an older portion of another individual. Parting at the seams between modules demonstrates that modules were stronger than the joins between them (Fig. 8). That this close proximity frequently occurs nearer the proximal ends of individuals is noteworthy. For a total of 62 specimens on 12 slabs, 49 are nearly parallel for most of their length, 13 of these pairs are touching at their margins and another 12 pairs display a significant amount of oblique overlap. This preferred alignment presents a striking contrast with other Ediacaran taxa that are routinely preserved as external moulds in negative hyporelief. For example, more than 160 well separated specimens of *Dickinsonia costata* occur on a 6 m^2 jig-sawed bed extracted from nearby Crisp Gorge (Reid *et al.* 2017). This contrast between *Dickinsonia* and *Phyllozoon* implies important differences in both biology and taphonomy between the two taxa. We suggest that *Phyllozoon* was a prostrate mat dweller that grew gregariously in such a way that individuals only slightly overlapped each other. *Dickinsonia*, on the other hand, was mobile enough to avoid the close proximity or even overlap that would inevitably result from the growth of closely spaced immobile juveniles (Reid *et al.* 2017).

The lens-shaped sand-filled tubes of *Aulozoon* (Figs 5, 8–10; online Supplementary Fig. S2) may occasionally be separated from bed bases, revealing wrinkle marks on both sides of the extracted

sausage-shaped tubes. Sawn sections show that the sand within the tubes is identical to that of the bed that buried them (Fig. 10), suggesting that the sand entered the tubes during the process of burial rather than by active incorporation. Some of the individuals on the studied slab are the largest known, reaching at least 1 m in observed length. The complex manner in which individuals of *Aulozoon* are interwoven shows that *Aulozoon* was a coherent, flexible tubular body fossil, not the mucus-lined gallery of a burrow like the early Cambrian trace fossil *Plagiogmus* Roedel, 1929 (McIlroy & Heys, 2008). Haematitic silt, which separates the sand-filled tubes from the bed soles, may have been derived from an original pyritic film that seems to have stiffened many Ediacaran organic materials during decay (Gehling, 1999). The physical integrity of the *Aulozoon* tubes and their pattern of deformation imply a secreted tissue rather than an agglutinated grade of construction.

The putative traces, *Dickinsonia* 'footprints' and *Kimberichnus* scratch marks must be both benthic and formed *in situ* if they are really trace fossils (Gehling *et al.* 2014; Evans *et al.* 2019). The fact that *Kimberichnus* is superimposed on *Phyllozoon* (online Supplementary Fig. S3a) could be regarded as evidence that the *Phyllozoon* fronds were not prostrate lichens inhabiting the matground (Retallack, 2007), but instead were transported prior to burial by the overlying bed. However, it is also possible the scratches were cut through the *Phyllozoon* frond. The situation with the *Dickinsonia* 'footprints' is equally puzzling, because in all four cases the 'footprints' are interrupted by *Aulozoon* tubes (Fig. 5, A–D). At first, it is difficult to imagine that the sandy tubes could have eliminated any trace of the pre-existing concave footprints during burial, but there seem to be only five possibilities: (1) the footprints pre-date the sandy tubes and were partly obliterated by them; (2) the footprints post-date the deposition of the sandy tubes; (3) the footprints are transported body fossils, not trace fossils, and they overlie the tubes; (4) the footprints are the bounce marks of bodies carried by currents and then moved on again; or (5) the sandy tubes are compacted horizontal burrows within the event bed, and not body fossils. The last alternative is discussed above and rejected.

The preservation of the footprints as effaced, convex hyporelief structures is similar to that seen at other sites, most notably those on the IT-NA surface of the Nilpena precinct, where a long series of overlapping footprints is strong evidence for the trace fossil interpretation (Evans *et al.* 2019). Perhaps the most likely scenario for the Bathtub 'footprints' is that they were already on the matground and were overwritten by the sand-filled tubes, which settled quickly like gravel clasts prior to any sand grains during the storm surge event. As a result, there was no sediment between tube and the footprint to record the presence of the former beneath the latter. Although only some *Aulozoon* tubes are clearly underlain by *Phyllozoon* fronds (Fig. 10; online Supplementary Fig. S3d), those *Phyllozoon* that are interrupted by *Aulozoon* (Figs 5, 8, 10; online Supplementary Fig. S3b, c) may therefore also have been underneath the tubes. The difference in preservation may simply be a result of the amount of surge sand that ended up between the frond and the tube. This is well shown by the two highlighted *Aulozoon* tubes in Figure 10; the holotype (black arrows) interrupts the *Phyllozoon* fronds because it was laid down directly on them, and the other *Aulozoon* (white arrows) is a sand-filled sausage within the event bed, meaning that the sediment underneath it could record the passage of the fronds where they crossed the tube. In this and other cases, sediment within the tubes was able to cast underlying specimens of *Phyllozoon* leaving a composite impression of both taxa (online Supplementary Fig. S3d). Where

specimens of *Phyllozoon* are interrupted by *Aulozoon* tubes (Figs 5, 8; online Supplementary Figs S2, S3b,c), it has been assumed that the former overlies the latter (Gehling *et al.* 2005). This is also suggested in some cases by the way the bed base curves inwards (upwards) as the *Phyllozoon* approaches and leaves the *Aulozoon* tube. A reviewer suggested testing this hypothesis by removing a section of a sandy *Aulozoon* tube to expose part of an overlying *Phyllozoon*. This was performed (online Supplementary Fig. S3b, c) and the hypothesis was falsified; there is no trace of *Phyllozoon* above the sand-filled tube (online Supplementary Fig. S3c). We therefore conclude that, of the five alternatives, option (1) is correct; the sandy tubes of *Aulozoon* obscure underlying body and trace fossils because they were deposited on them without any intervening sediment. A benthic community represented by *Phyllozoon* fronds and *Dickinsonia* 'footprints' was therefore overprinted with a death assemblage of *Aulozoon* sandy tubes carried in by the storm surge that deposited the Bathtub slab event bed.

3.d. Discussion and taphonomic conclusions

In summary, this snapshot of the sea floor was captured by a thin sandy event bed deposited by the waning phase of a storm surge in a deep subtidal environment. The surface on which the event bed was deposited was a well developed matground inhabited by numerous prostrate *Phyllozoon* fronds, scattered individuals of *Dickinsonia costata*, the producer of the *Kimberichnus* scratch marks and rare examples of a few other common Ediacaran taxa. During the surge, evacuated *Aulozoon* tubes were washed in and those that had been infiltrated with sand sank to the bottom first at the speed of gravel clasts. Following deposition of the sandy component of the storm surge, the hydrostatic skeletons of the fluid- or tissue-filled *Phyllozoon* fronds collapsed so that the bodies are preserved as convex hyporelief casts on the fine sandstone bed base. This then is a snapshot of a death assemblage of *in situ* and *ex situ* organisms that may all have had a patchy distribution on this subtidal sea floor.

4. Systematic palaeontology

Orphan plesion Erniettomorpha Pflug, 1972

Discussion. The higher taxonomy of Ediacaran soft-bodied organisms is in a state of flux but there is widespread agreement that the Namibian genera *Pteridinium* Gürich, 1933 and *Ernietta* Pflug, 1966 are sufficiently closely related to be included in the same extinct clade, the Erniettomorpha Pflug, 1972. This 'orphan plesion' may also include *Phyllozoon*, in the sense that *Phyllozoon* is something like a two-vaned *Pteridinium* (Jenkins & Gehling, 1978).

Phyllozoon Jenkins & Gehling, 1978

Type species. Phyllozoon hanseni Jenkins & Gehling, 1978, by original designation and monotypy.

Phyllozoon hanseni Jenkins & Gehling, 1978

Figs 5–8; online Supplementary Figs S1, S3, S4.

1978 *Phyllozoon hanseni* Jenkins & Gehling, pp. 357–58, fig. 7.
1991 *Phyllozoon hanseni* Jenkins and Gehling; Gehling, pl. 3, fig. 2.
1992 *Phyllozoon* Jenkins and Gehling; Runnegar, fig. 3.10.
1994 *Phyllozoon hanseni* Jenkins and Gehling; Runnegar, fig. 3.
2003 *Phyllozoon hanseni* Jenkins and Gehling; Seilacher, Grazhdankin & Legouta, pp. 45–46, Fig. 5.

2005 *Phyllozoon* Jenkins and Gehling; Gehling, Droser, Jensen & Runnegar, p. 51, Fig. 5.

2005 *Phyllozoon* Jenkins and Gehling; Seilacher, Buatois & Mángano, pp. 328–29, Fig. 4.

2007 *Phyllozoon* Jenkins and Gehling; Seilacher, p. 178, pl. 62.

2007 *Phyllozoon hanseni* Jenkins and Gehling; Jenkins & Nedin, p. 209, Fig. 8c.

2007 *Phyllozoon hanseni* Jenkins and Gehling; Retallack, p. 17, Fig. 7.

Type material. SAM P19508A (holotype) and P19508B-C (paratypes), all on same slab, Nilpena Sandstone Member, Rawnsley Quartzite, The Devil's Peak, south of Quorn, southern Flinders Ranges; 32.414995° S, 137.991176° E (Jenkins & Gehling, 1978, Fig. 7).

Revised diagnosis. Frond elongate and biserial, rounded at the presumed proximal end, parallel sided for some distance then tapering to a narrow distal growing tip formed of progressively narrower and shorter modules. Frond constructed entirely from straight to slightly curved units (collapsed tubular modules), gently convex in profile on bed bases, alternating in a zig-zag fashion across the midline, and extending at 70–90° to it; adjacent ribs are separated by well defined narrow grooves; marginal terminations of modules rounded, often indistinct; first three to five modules of proximal region of frond short and wide; others decrease in size gradually away from the proximal end of frond but maintain approximately equal length perpendicular to axis until frond begins to taper distally.

Distribution. The type locality, The Devil's Peak, is *c.* 140 km SSW of Bathtub Gorge (Fig. 1). Apart from these two sites, *Phyllozoon* has been recorded from 30 localities throughout the central Flinders Ranges, including several with measured stratigraphic sections. These include the Nilpena Sandstone Member (Mayo Gorge, Chace Range, Tooth's Nob, Nilpena precinct of the Ediacara Conservation Park); specimens have also been photographed from stratigraphic levels well above the richly fossiliferous Ediacara Sandstone Member beneath Mount Abrupt and within Tea Cosy Gorge, north of Bathtub Gorge (Fig. 1). Notably, *Phyllozoon* has not been recovered from the Ediacara Hills sector of the Conservation Park, *c.* 20 km north of Nilpena (Fig. 1).

Description. *Phyllozoon* is an elongate strap-shaped frondose organism with the presumed proximal end being more rounded and wider than the tapering distal end, where the addition of new tubular modules probably occurred. Both the midline and boundaries between collapsed modules form sharp grooves, suggesting quilting. The peripheral ends of the modules are generally imprecisely defined. The boundaries of the modules are slightly curved in the plane of the bed, and weakly concave toward the narrower, apical end of the frond. With the exception of near the proximal end, the modules are relatively constant in length (axis to margin) for much of the frond but decrease in length for the distal third. The incomplete holotype is 18 cm long and 5.5 cm at the widest point. Six nearly complete specimens from Bathtub Gorge vary in length from 21 to 26 cm (average 23.5 cm) and from 3.8 to 4.2 cm (average 4 cm) in maximum width. The average length and width of complete specimens from all localities is 24.1 cm and 3.9 cm, respectively. Complete specimens have 80–100 modules on each side (online Supplementary Fig. S1), varying in width from 1 to 5 mm (average 2.1 mm).

Discussion. *Phyllozoon* does not seem to be an upright frondose or petaloid form, as previously inferred by Jenkins & Gehling (1978). Over-printing by examples of well-known Ediacaran taxa

(e.g. Fig. 6) implies that *Phyllozoon* was arrayed as recumbent gregarious sets of prostrate fronds at the time of burial. There is no evidence of a point of attachment, rachis or stolon. Modules were probably simple tubes lacking partitions, and joined laterally and at the zig-zag axis. Cumulative widths of modules plotted against number of modules gives a growth curve that is slightly negatively allometric (online Supplementary Fig. S1). The only suggestion that the modules were not closed distally is the often poor preservation of their peripheral ends. However, evidence for air-mattress-like hydrostatic strength (Fig. 8) – the 'quilted pneu' of Seilacher (1992) – makes that improbable.

Phyllozoon is also found at other places in the Flinders Ranges (Fig. 6; online Supplementary Fig. S4) but at almost all other sites is not associated with *Aulozoon*. On the other hand, *Aulozoon* occurs at Ediacara in the Mount Scott Range (Fig. 10) and in a number of other areas without *Phyllozoon*. These separations negate the idea that *Phyllozoon* might somehow be part of the inhabitant of *Aulozoon* tubes. However, several other sites do show the 'hugging' that seems characteristic of *Phyllozoon* and also an association with *Dickinsonia* footprints and body fossils (Fig. 6). This seems to be a characteristic feature of its gregarious habit.

Unlike *Pteridinium* from Namibia (Pflug, 1970), Russia (Fedonkin, 1992), North Carolina (Gibson *et al.* 1984), Ediacara (Glaessner & Wade, 1966) and Nilpena (Gehling & Droser, 2013), a third ribbed vane is not present in *Phyllozoon* (Jenkins & Gehling, 1978). Like other erniettomorphs, *Phyllozoon* lacks evidence for discrete structures smaller than the modules. Resolution of its affinities will require a fuller understanding of the whole clade.

Orphan plesion Dickinsoniomorpha Erwin *et al.* 2011

Genus *Dickinsonia* Sprigg, 1947

Type species. Dickinsonia costata Sprigg, 1947, by monotypy.

Dickinsonia rex Jenkins, 1992

Online Supplementary Figs S5, S6.

1972 *Dickinsonia elongata* Glaessner and Wade, 1966; Wade, p. 178, pl. 7, Fig. 2.

1992 *Dickinsonia elongata* Glaessner and Wade, 1966; Runnegar & Fedonkin, p. 383, Fig. 7.5.7D.

2005 *Dickinsonia rex* Jenkins, 1992; Gehling, Droser, Jensen & Runnegar, p. 51, Fig. 4.

Type material. Holotype, SAM P18086 (Wade, 1972, pl. 2, Fig. 2) probably from the base of the Nilpena Sandstone Member, Rawnsley Quartzite, Brachina Gorge, Heysen Range; 31.342481° S, 138.569593° E; specimen collected by RJF Jenkins prior to 1972. De facto paratype (Fig. 6b), specimen illustrated by Jenkins (1992, fig. 14) from the base of thick sandstone bed at the 7.5 m level (section 1, Figs 3, 4a), Nilpena Sandstone Member, Rawnsley Quartzite, Bathtub Gorge; 31.245011° S, 138.538350° E. This significant figured specimen remains in the field (last seen 24 May 2005); two unregistered plaster casts of it are currently held in the palaeontological collection of the South Australian Museum.

Description. Large, stadium-shaped species of *Dickinsonia* with numerous closely spaced modules. The holotype has the tail end folded over but Wade (1972) estimated its length as 38–39 cm and width *c.* 14 cm, a L/W ratio of *c.* 1.5 compared with a L/W of *c.* 1 for *D. costata* (Evans *et al.* 2017). Capable of growth to extraordinary sizes (*c.* 750 mm; online Supplementary Fig. S5) and, in larger specimens, having the outer edges of the modules expanded and imbricated. This feature is strikingly obvious in SAM P40168 (Gehling *et al.* 2005, fig. 4), a huge intact individual *c.* 840 mm in length that is part of the permanent display at the South Australian Museum. In this specimen the modules are

expressed as a closely spaced curved or even sinuous ridges and the module boundaries as deep grooves. The midline is crisp but exceedingly narrow for the size of the specimen, and there is no topographic evidence for a coincident internal organ. Where the distal edges of the modules flare and imbricate, there are ridges on the module walls approximately midway between the original dorsal and ventral surfaces. The edges of the specimen are expanded or withdrawn at a number of places on the periphery, presumably from perimortem processes. The number of modules is *c.* 400.

Distribution. As for *Phyllozoon hanseni*, *D. rex* may be confined to the Nilpena Sandstone Member of the Rawnsley Quartzite (Gehling *et al.* 2019). The holotype came from 'high in the cliff' in Brachina Gorge (Wade, 1972, p. 178), and the in-place topotype shown in online Supplementary Figure S5 is from the base of a 25 cm thick sandstone at the approximate position of the lowest occurrence of facies 7 in the Brachina Gorge section of McMahon *et al.* (2021, fig. 3). Both occurrences are low in the Nilpena Sandstone Member. Elsewhere, *D. rex* occurs within the Nilpena Sandstone Member at Nilpena (Gehling *et al.* 2019), Bathtub Gorge (online Supplementary Fig. S6a, available at http://journals.cambridge.org/geo) and in the Chace Range (online Supplementary Fig. S6b), where it occurs with *Arkarua adami* Gehling, 1987 and *Inaria karli* Gehling, 1988 in measured section S31, east end of the range (Fig. 1; Gehling, 1987, 2000).

Discussion. Glaessner & Wade (1966) proposed *Dickinsonia elongata* for elongate species of *Dickinsonia* that taper slightly posteriorly. They illustrated only the holotype (SAM P13767) that, although 16 cm long, they regarded as juvenile in comparison with incomplete specimens that were 30–40 cm in length. However, Jenkins (1992) considered the holotype to be a poorly preserved specimen of *D. costata* (we concur), so *elongata* became a subjective junior synonym of *costata* and the name *elongata* should be restricted to its holotype. For the larger elongate examples of *Dickinsonia*, Jenkins (1992) introduced the specific epithet *rex* that he described as a new name rather than a new species. Perhaps for this reason, the taxonomic status of *D. rex* has seemed unclear. This brief re-description is aimed at eliminating any uncertainty about the validity of the species.

When Jenkins (1992) proposed *D. rex*, he did not provide a systematic description of the new species because *elongata* had previously been well described by Glaessner & Wade (1966) and Wade (1972). At the time, there was a community understanding of the species *elongata*, based on specimens from Ediacara and Brachina Gorge. However, the unfortunate choice of an unrepresentative holotype because it was 'a juvenile specimen with both anterior and posterior ends' (Glaessner & Wade, 1966, p. 621) required suppression of the name. Equally unfortunately, only the holotype of *elongata* was figured in 1966 and the paratypes were not listed by SAM P number. A similar situation pertained in 1972, when Wade mentioned two almost-complete adult specimens from Brachina Gorge but figured only one, the holotype of *D. rex* (Wade, 1972, pl. 7 fig. 2). When Jenkins (1992) proposed *D. rex* as a replacement name for *D. elongata*, only two specimens of the then well understood species had therefore been illustrated. For this reason, the specimen figured by Jenkins (1992, fig. 14) from Bathtub Gorge (Fig. 6b) serves as a de facto paratype of *D. rex*.

Some individuals of *Dickinsonia costata* grew to a substantial size (Runnegar, 2021, fig. 4b) but nowhere near the size of the largest individuals of *D. rex* (online Supplementary Fig. S6; Gehling *et al.* 2005, fig. 4). Furthermore, *D. costata* maintains an almost 1:1 L/W ratio throughout growth in contrast to *D. rex*

(Runnegar, 1982; Evans *et al.* 2017). *Dickinsonia tenuis* Glaessner & Wade (1966) is another large species of *Dickinsonia*, but it is more equidimensional (L/W *c.* 1.3) and had approximately three times as many modules per unit length than *rex*. Small specimens of *D. tenuis* and *D. rex* may be difficult to tell apart; however, in large specimens the differences are obvious because of the difference in proportions and the spacing of the modules. *Dickinsonia lissa* Wade, 1972 is even more elongate (L/W *c.* 3) and has a very large number of narrow modules and a prominent axial ridge, features that are also obvious in Russian members of this species (Ivantsov, 2007). The great differences in proportions and module size readily distinguish *lissa* from *rex*.

Phylum Annelida Lamarck, 1809?

Genus *Aulozoon* gen. nov.

Type species. Aulozoon solorium sp. nov.

Derivation of name. From *aulos*, Greek, flute or pipe and *zoön*, Greek, animal.

Diagnosis. Large, cylindrical, unmineralized, flexible tube, one to several centimetres in diameter and up to at least 1 m in length, often with at least one rounded end, typically preserved in slightly to significantly convex hyporelief as empty or partly sand-filled structures; straight, looped or coiled, lenticular or D-shaped in cross-section, and separated from surrounding matrix by ferruginous quartz silt.

1969 Form D Glaessner, pp. 381–2, Fig. 5E.

1995 *Palaeophycus tubularis* Hall, 1847; Jenkins, pp. 56–8, pl. 1F.

2003 *Aulozoon* (*nomen nudum*); Seilacher, Grazhdankin & Legouta, pp. 45–50, Fig. 5.

2005 *Aulozoon* (*nomen nudum*); Seilacher, Buatois & Mángano, pp. 328–29, Fig. 4.

2005 Form D Glaessner; Droser, Gehling & Jensen, pp. 134–5, Fig. 5.

2007 *Aulozoon* (*nomen nudum*); Seilacher, p. 178, pl. 62.

2007 *Aulozoon* (*nomen nudum*); Retallack, p. 17, Fig. 7.

2015 *Aulozoon* (*nomen nudum*); Seilacher & Gishlick, p. 142.

Aulozoon solorium sp. nov.

Figs 5, 8–10; online Supplementary Figs S2, S3b–d.

Derivation of name. From *solium*, Latin, bathtub; genitive plural because Bathtub Gorge has many bathtubs (waterholes).

Discussion. This new genus and species was described as *Aulozoon arteria* Gehling (Gehling, 1996). The generic name was adopted informally by Seilacher *et al.* (2003, 2005) and thus became by definition a *nomen nudum*, lacking a designated type specimen and an adequate description and definition. Here, we rectify that situation.

Type material. Holotype, SAM P35690A, part (Figs 8, 9) and SAM P35690B, counterpart; paratype, SAM P58400 (online Supplementary Fig. S2), all from the same surface (Fig. 5), Nilpena Sandstone Member, Bathtub Gorge; 31.245011° S, 138.538350° E; paratype, SAM P58399A–D (Fig. 10), Rawnsley Quartzite, Mount Scott Range, via Leigh Creek, South Australia; 30.621092° S, 138.356203° E (Fig. 1).

Description. Aulozoon is a tubular body fossil, probably originally circular in cross-section, that varies in diameter from *c.* 1–3 cm and is normally preserved in convex hyporelief on bed bases. The full length is unknown, but some individuals exceed *c.* 1 m. Individuals on the same surface frequently overlap and cross each other, but do not merge at intersections. Unfilled tubes are flat or slightly convex in hyporelief and have sharply incised margins. Tubes are generally sinuous, or make broad loops with a radius of turn roughly proportional to the tube width (Figs 4–6). Angular

bends in the loops involve marked kinking on the inside of the turns (Figs 6, 7). The margins are smooth in straight or sinuous specimens, but more irregular or slightly scalloped on some loops and near poorly preserved terminations. The surface of specimens varies from smooth and featureless to transversely or obliquely wrinkled with sharp grooves that are most prominent on the inside of the bends. Wrinkle marks are more common in sand-filled specimens close to the basal rounded termination, when preserved, than on the hyporelief casts of unfilled tubes. A deep, discontinuous, median longitudinal groove occurs on parts of some specimens without transverse wrinkles. Apparent terminations are simple and rounded, but may only represent the point at which the tube curved upwards into the bed that buried it or where the sediment fill ended.

Distribution. Aulozoon soliorum *is a common fossil at Ediacara and is widespread in the Flinders Ranges. We illustrate specimens from Bathtub Gorge and the Mount Scott Range (Fig. 1), but it occurs at many other sites in both the Ediacara and Nilpena members of the Rawnsley Quartzite.*

Discussion. In a review of the then known Ediacaran and early Cambrian trace fossils, Glaessner (1969) identified *Aulozoon soliorum* as vermiform burrow, which he called 'Form D'. Runnegar & Fedonkin (1992) and Fedonkin & Runnegar (1992) recognized the three-dimensional nature of these fossils, and suggested that they may have been mucilaginous tubes made by worm-like metazoans. A sediment-filled specimen was illustrated by Jenkins (1995, pl. 1F) as the trace fossil *Palaeophycus tubularis* Hall, 1847, but there is really no close similarity; *Aulozoon* differs from *Palaeophycus* in its lack of burrow junctions, more uniform cylindrical shape and the fact that it never branches. Other previous references to *Aulozoon soliorum* as the *nomen nudum* 'Aulozoon' are discussed in Section 3.

Several of Glaessner's (1969) trace fossils have turned out to be tubular body fossils (Droser *et al.* 2005; Sappenfield *et al.* 2011). One of these, *Somatohelix sinuosis*, overlaps the size range of *Aulozoon soliorum* but *Somatohelix* – as the name suggests – was helically coiled, albeit at a long wavelength. No evidence of systematic curving or coiling is present in the tubes of *Aulozoon*. The only other form that is comparable to *Aulozoon soliorum* seems to be *Vittatusivermis annularius* from the earliest Cambrian Period of China (Zhang *et al.* 2017). Although clearly a body fossil, the tube of *Vittatusivermis* is finely annulated and, in one case, twisted through 180°. Neither of these features is seen in *Aulozoon*.

Runnegar (1994) discussed the resemblance of *Aulozoon* to the tubes of the living vestimentiferan annelid, *Riftia pachyptila*. Tubes of *Riftia*, described by Jones (1980) from the Galápagos Rift on the East Pacific Rise, share the same dimensional proportions, basal blind ending, transverse wrinkles and manner of kinking as *Aulozoon* but, in the absence of any evidence of the nature of the inhabitant of the *Aulozoon* tubes, the significance of the similarities is difficult to assess. *Riftia* tubes are cylindrical, fast growing from both ends (tens of cm^{-1}), constructed of chitin (*c.* 33%) and protein, but also have complications such as basal septa and forking not seen in *Aulozoon* (Gaill & Hunt, 1986; Gaill *et al.* 1997). In the related vestimentiferan *Teunia jerichonana*, the tube is formed from criss-crossed ribbons of fibrous chitin arranged in a 'nematic' fashion (Gaill *et al.* 1992). This arrangement is similar to that seen in the Ediacaran fossil *Sabellidites cambriensis*, which Moczydłowska *et al.* (2014) interpreted to be the tube of a siboglinid, and perhaps a vestimentiferan annelid worm. Comparable worm tubes attributed to annelids have a substantial

Phanerozoic record (Georgieva *et al.* 2019), and most of the Ediacaran–Terreneuvian cylindrical body fossils of Budd's 'tube world' (Budd & Jackson, 2016), whether mineralized or not, are now thought to be stem or crown annelids (Yang *et al.* 2020). It is therefore plausible to regard an annelid affinity for *Aulozoon* as the null hypothesis. Recent discoveries of widespread methane leaks from oceanic seafloor sediments (Goffredi *et al.* 2020) makes a chemosymbiotic lifestyle for the inhabitant of *Aulozoon* tubes a possibility.

5. Conclusions

The event bed with *Phyllozoon* and *Aulozoon* in Bathtub Gorge is an example of an assemblage that is younger and different from the classical fossiliferous horizons of the older Ediacara Sandstone Member. Because the site is in a deep gorge that cuts the Heysen Range, only one small *c.* 1 m² window was amenable for study. Despite this limitation, it is clear that this event bed preserves a time-lapse video of the depositional environment and its ecology, rather than a single snapshot. The deeply subtidal matground that developed during quiet stable conditions was inhabited by patchy gregarious aggregations of prostrate *Phyllozoon* fronds and some dispersed members of other clades, including the animals that made the *Dickinsonia* cf. *costata* 'footprints' and the *Kimberichnus teruzzi* scratch traces. During an energetic storm surge, vacated sand-filled tubes of *Aulozoon soliorum* were carried in and deposited swiftly, falling like pebbles rather than sand grains. As a result, their lower surfaces did not replicate the parts of the *Phyllozoon* fronds that lay beneath them, giving the impression when seen from the bed sole side that the fronds were above the tubes. In fact, all *Aulozoon* tubes probably overlie all *Phyllozoon* fronds, meaning that this is an example of an *in situ* life assemblage overprinted by an *ex situ* death assemblage. Exactly how *Phyllozoon* and *Aulozoon* lived and operated remains unclear, and their biological affinities are still obscure. However, *Phyllozoon* is almost certainly a member of the orphan plesion Erniettomorpha – which includes *Pteridinium* and *Ernietta* – and *Aulozoon* is not.

References

Betts MJ, Paterson JR, Jacquet SM, Andrew AS, Hall PA, Jago JB, Jagodzinski EA, Preiss WV, Crowley JL, Brougham T, Mathewson CP, García-Bellido DC, Topper TP, Skovsted CB and Brock GA (2018) Early Cambrian chronostratigraphy and geochronology of South Australia. *Earth-Science Reviews* **185**, 498–543.

Billings E (1872) Fossils in Huronian rocks. *Canadian Naturalist and Quarterly Journal of Science* **6**, 478.

Budd GE and Jackson ISC (2016) Ecological innovations in the Cambrian and the origins of the crown group phyla. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**, 20150287.

Coutts FJ, Gehling JG and García-Bellido DC (2016) How diverse were early animal communities? An example from Ediacara Conservation Park, Flinders Ranges, South Australia. *Alcheringa: An Australasian Journal of Palaeontology* **40**, 407–21.

Daily B (1973) Discovery and significance of basal Cambrian Uratanna Formation, Mt Scott Range, Flinders Ranges, South Australia. *Search* **4**, 202–5.

Droser ML and Gehling JG (2008) Synchronous aggregate growth in an abundant new Ediacaran tubular organism. *Science* **319**, 1660–2.

Droser ML, Gehling JG and Jensen SR (2005) Ediacaran trace fossils: true and false. In *Evolving Form and Function: Fossils and Development: Proceedings of a Symposium Honoring Adolf Seilacher for his Contributions to Paleontology, In Celebration of his 80th Birthday* (ed. DEG Briggs), pp. 125–38. New Haven: Peabody Museum of Natural History, Yale University.

Droser ML, Gehling JG and Jensen SR (2006) Assemblage palaeoecology of the Ediacara biota: The unabridged edition? *Palaeogeography, Palaeoclimatology, Palaeoecology* **232**, 131–47.

Erwin DH, Laflamme M, Tweedt SM, Sperling EA, Pisani D and Peterson KJ (2011) The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* **334**, 1091–7.

Evans SD, Droser ML and Gehling JG (2017) Highly regulated growth and development of the Ediacara macrofossil Dickinsonia costata. *PLoS ONE* **12**, e0176874.

Evans SD, Dzaugis PW, Droser ML and Gehling JG (2016) You can get anything you want from Alice's Restaurant Bed: exceptional preservation and an unusual fossil assemblage from a newly excavated bed (Ediacara Member, Nilpena, South Australia). *Australian Journal of Earth Sciences* **67**, 873–83.

Evans SD, Gehling JG and Droser ML (2019) Slime travelers: early evidence of animal mobility and feeding in an organic mat world. *Geobiology* **17**, 490–509.

Fedonkin MA (1992) Vendian faunas and early evolution of Metazoa. In *Origin and Early Evolution of the Metazoa* (eds JH Lipps and PW Signor), pp. 87–129. New York: Plenum Press.

Fedonkin MA and Runnegar B (1992) Proterozoic metazoan trace fossils. In *The Proterozoic Biosphere, A Multidisciplinary Study* (eds JW Schopf and C Klein), pp. 389–95. New York: Cambridge University Press.

Feng T, Chongyu YIN, Bengtson S, Pengju LIU, Ziqiang W and Linzhi GAO (2008) Octoradiate spiral organisms in the Ediacaran of South China. *Acta Geologica Sinica – English Edition* **82**, 27–34.

Gaill F and Hunt S (1986) Tubes of deep sea hydrothermal vent worms *Riftia pachyptila* (Vestimentifera) and *Alvinella pompejana* (Annelida). *Marine Ecology Progress Series* **34**, 267–74.

Gaill F, Persson FJ, Sugiyama J, Vuong R, and Chanzy H (1992) The chitin system in the tubes of deep sea hydrothermal vent worms. *Journal of Structural Biology* **109**, 116–28.

Gaill F, Shillito B, Ménard F, Goffinet G and Childress JJ (1997) Rate and process of tube production by the deepsea hydrothermal vent tubeworm *Riftia pachyptila*. *Marine Ecology Progress Series* **148**, 135–43.

Gehling JG (1987) Earliest known echinoderm—a new Ediacaran fossil from the Pound subgroup of South Australia. *Alcheringa: An Australasian Journal of Palaeontology* **11**, 337–45.

Gehling JG (1988) A cnidarian of actinian-grade from the Ediacaran Pound Subgroup, South Australia. *Alcheringa: An Australasian Journal of Palaeontology* **12**, 299–314.

Gehling JG (1991) The case for Ediacaran fossil roots to the metazoan tree. *Geological Society of India Memoir* **20**, 181–224.

Gehling JG (1996) Taphonomy of the terminal Proterozoic Ediacara biota, South Australia. Unpublished Ph.D. dissertation, University of California, Los Angeles, 234 p.

Gehling JG (1999) Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios* **14**, 40–57.

Gehling JG (2000) Environmental interpretation and a sequence stratigraphic framework for the terminal Proterozoic Ediacara Member within the Rawnsley Quartzite, South Australia. *Precambrian Research* **100**, 65–95.

Gehling JG and Droser ML (2013) How well do fossil assemblages of the Ediacara biota tell time? *Geology* **41**, 447–50.

Gehling JG, Droser ML, Jensen SR and Runnegar B (2005) Ediacaran organisms: relating form and function. In *Evolving Form and Function: Fossils and Development: Proceedings of a Symposium Honoring Adolf Seilacher for his Contributions to Paleontology, in Celebration of his 80th Birthday* (ed. DEG Briggs), pp. 43–67. New Haven: Peabody Museum of Natural History, Yale University.

Gehling JG, García-Bellido DC, Droser ML, Tarhan LG and Runnegar B (2019) The Ediacaran-Cambrian transition: sedimentary facies versus extinction. *Estudios Geológicos* **75**, e099.

Gehling JG and Rigby JK (1996) Long expected sponges from the Neoproterozoic Ediacara fauna of South Australia. *Journal of Paleontology* **70**, 185–95.

Gehling JG, Runnegar B and Droser ML (2014) Scratch traces of large Ediacara bilaterian animals. *Journal of Paleontology* **88**, 284–98.

Georgieva MN, Little Crispin TS, Watson JS, Sephton MA, Ball AD and Glover AG (2019) Identification of fossil worm tubes from Phanerozoic hydrothermal vents and cold seeps. *Journal of Systematic Palaeontology* **17**, 287–329.

Gibson GG, Teeter SA and Fedonkin MA (1984) Ediacarian fossils from the Carolina slate belt, Stanly Country, North Carolina. *Geology* **12**, 387–90.

Glaessner MF (1969) Trace fossils from the Precambrian and basal Cambrian. *Lethaia* **2**, 369–93.

Glaessner MF and Daily B (1959) The geology and late Precambrian fauna of the Ediacara fossil reserve. *Records of the South Australian Museum* **13**, 369–401.

Glaessner MF and Wade M (1966) The late Precambrian fossils from Ediacara, South Australia. *Palaeontology* **9**, 599–628.

Goffredi SK, Tilic E, Mullin SW, Dawson KS, Keller A, Lee RW, Wu F, Levin LA, Rouse GW, Cordes EE and Orphan VJ (2020) Methanotrophic bacterial symbionts fuel dense populations of deep-sea feather duster worms (Sabellida, Annelida) and extend the spatial influence of methane seepage. *Science Advances* **6**, 14.

Gürich G (1933) Die Kuibis-Fossilien der Nama-Formation von Südwestafrika. *Paläontolische Zeitschrift* **15**, 137–154.

Hall J (1847) *Palaeontology of New York, volume 1. Containing descriptions of the organic remains of the Lower Division of the New York System (equivalent to the Lower Silurian rocks of Europe)*. Albany, New York: C. van Benthuysen, 338 p.

Ivantsov A Yu (2007) Small Vendian transversely articulated fossils. *Paleontological Journal* **41**, 113–22.

Ivantsov A Yu (2011) Feeding traces of Proarticulata—the Vendian Metazoa. *Paleontological Journal* **43**, 237–48.

Ivantsov A Yu (2013) Trace fossils of Precambrian Metazoa "Vendobionta" and "Mollusks". *Paleontological Journal* **21**, 252–64.

Ivantsov A Yu and Malakhovskaya IE (2002) Gigantic traces of Vendian invertebrate animals. *Doklady Akademii Nauk SSSR* **385**, 382–6.

Jago JB, Gehling JG, Betts MJ, Brock GA, Dalgarno CR, García-Bellido DC, Haslett PG, Jacquet SM, Kruse PD, Langsford NR, Mount TJ and Paterson JR (2020) The Cambrian System in the Arrowie Basin, Flinders Ranges, South Australia. *Australian Journal of Earth Sciences* **67**, 923–48.

Jago JB, Sun X and Zang W (2002) The most probable Eumetazoa among late Precambrian macrofossils. *Invertebrate Zoology* **14**, 127–33.

Jenkins RJF (1992) Functional and ecological aspects of Ediacaran assemblages. In *Origin and Early Evolution of the Metazoa* (eds JH Lipps and PW Signor), pp. 131–76. New York: Plenum Press.

Jenkins RJF (1995) The problems and potential of using animal fossils and trace fossils in terminal Proterozoic biostratigraphy. *Precambrian Research* **73**, 51–69.

Jenkins RJF and Gehling JG (1978) A review of frond-like fossils of the Ediacara assemblage. *Records of the South Australian Museum* **17**, 347–59.

Jenkins RJF and Nedin C (2007) The provenance and palaeobiology of a new multi-vaned, chambered frondose organism from the Ediacaran (later Neoproterozoic) of South Australia. In *The Rise and Fall of the Ediacaran Biota* (eds P Vickers-Rich and P Komarower), pp. 195–222. Geological Society of London, Special Publication no. 286.

Jones M (1980) *Riftia pachyptila*, new genus, new species, the vestimentiferan worm from the Galápagos Rift geothermal vents (Pogonophora). *Proceedings of the Biological Society of Washington* **93**, 1295–313.

Lamarck JBPA de M (1809) *Philosophie Zoologique, ou exposition des considérations relative à l'Histoire naturelle des animaux.* Paris: Musée d'Histoire Naturelle, 421 p.

McIlroy D and Heys GR (2008) Palaeobiological significance of *Plagiogmus arcuatus* from the lower Cambrian of central Australia. *Alcheringa* **21**, 161–78.

McMahon WJ, Liu AG, Tindal BH and Kleinhans MG (2021) Ediacaran life close to land: coastal and shoreface habitats of the Ediacaran macrobiota, the Central Flinders Ranges, South Australia. *Journal of Sedimentary Research* **90**, 1463–99.

Moczydłowska M, Westall F and Foucher F (2014) Microstructure and biogeochemistry of the organically preserved Ediacaran metazoan *Sabellidites*. *Journal of Paleontology* **88**, 224–39.

Pflug HD (1966) Neue Fossilreste aus den Nama-Schichten in Südwest-Afrika. *Paläontologische Zeitschrift* **40**, 14–25.

Pflug HD (1970) Zur Fauna der Nama-Schichten in Südwest-Afrika. I. Zur Fauna der Nama-Schichten in Südwest-Afrika. I. Pteridinia, Bau und systematische Zugehörigkeit. *Palaeontographica* **A134**, 153–262.

Pflug HD (1972) Zur Fauna der Nama-Schichten in Südwest-Afrika. III. Erniettomorpha, Bau und Systematik. *Palaeontographica* **A139**, 134–170.

Reid LM, García-Bellido DC, Payne JL, Runnegar B and Gehling JG (2017) Possible evidence of primary succession in a juvenile-dominated Ediacara fossil surface from the Flinders Ranges, South Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **476**, 68–76.

Retallack GJ (2007) Growth, decay and burial compaction of *Dickinsonia*, an iconic Ediacaran fossil. *Alcheringa: An Australasian Journal of Palaeontology* **31**, 215–40.

Retallack GJ (2013) Ediacaran life on land. *Nature* **493**, 89–92.

Retallack GJ (2016) Ediacaran fossils in thin-section. *Alcheringa: An Australasian Journal of Palaeontology* **40**, 583–600.

Roedel H (1929) Ergänzung zu meiner Mitteilung über ein kambrisches Geschiebe mit problematischen Spuren. *Zeitschrift für Geschiebeforschung* **5**, 48–52.

Runnegar B (1982) Oxygen requirements, biology and phylogenetic significance of the late Precambrian worm *Dickinsonia*, and the evolution of the burrowing habit. *Alcheringa: An Australasian Journal of Palaeontology* **6**, 223–39.

Runnegar B (1992) Evolution of the earliest animals. In *Major Events in the History of Life* (ed. JW Schopf), pp. 65–93. Boston: Jones and Bartlett.

Runnegar B (1994) Proterozoic eukaryotes: evidence from biology and geology. In *Early Life on Earth, Nobel Symposium No. 84* (ed. S Bengtson), pp. 287–97. New York: Columbia University Press.

Runnegar B (2021) Following the logic behind biological interpretations of the Ediacaran biotas. *Geological Magazine.* https://doi.org/10.1017/S0016756821000443

Runnegar B and Fedonkin MA (1992) Proterozoic metazoan body fossils. In *The Proterozoic Biosphere, A Multidisciplinary Study* (eds JW Schopf and C Klein), pp. 369–87. New York: Cambridge University Press.

Sappenfield A, Droser ML and Gehling JG (2011) Problematica, trace fossils and tubes within the Ediacara Member (South Australia): redefining the Ediacaran trace fossil record one tube at a time. *Journal of Paleontology* **85**, 256–65.

Seilacher A (1992) Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Journal of the Geological Society, London* **149**, 607–13.

Seilacher A (2007) *Trace Fossil Analysis.* Berlin and Heidelberg: Springer-Verlag, 226 p.

Seilacher A, Buatois LA and Mángano G (2005) Trace fossils in the Ediacaran–Cambrian transition: behavioral diversification, ecological turnover and environmental shift. *Palaeogeography, Palaeoclimatology, Palaeoecology* **227**, 323–56.

Seilacher A and Gishlick AD (2015) *Morphodynamics.* Boca Raton: CRC Press, Taylor & Francis Group, 490 p.

Seilacher A, Grazhdankin D and Legouta A (2003) Ediacaran biota: the dawn of animal life in the shadow of giant protists. *Paleontological Research* **7**, 43–54.

Sprigg RC (1947) Early Cambrian (?) jellyfishes from the Flinders Ranges, South Australia. *Transactions of the Royal Society of South Australia* **71**, 212–24.

Sprigg RC (1949) Early Cambrian "jellyfishes" of Ediacara, South Australia and Mount John, Kimberley district, Western Australia. *Transactions of the Royal Society of South Australia* **73**, 72–99.

Wade M (1968) Preservation of soft-bodied animals in Precambrian sandstones, South Australia. *Lethaia* **1**, 238–67.

Wade M (1972) *Dickinsonia*: polychaete worms from the Late Precambrian Ediacara fauna, South Australia. *Memoirs of the Queensland Museum* **16**, 171–90.

Xiao S, Droser ML, Gehling JG, Hughes IV, Wan B, Chen Z and Yuan X (2013) Affirming life aquatic for the Ediacara biota in China and Australia. *Geology* **41**, 1095–8.

Yang B, Steiner M, Schiffbauer JD, Selly T, Wu X, Zhang C and Liu P (2020) Ultrastructure of Ediacaran cloudinids suggests diverse taphonomic histories and affinities with non-biomineralized annelids. *Scientific Reports* **10**, 535.

Zhang X, Liu W, Isozaki Y and Sato T (2017) Centimeter-wide worm-like fossils from the lowest Cambrian of South China. *Scientific Reports* **7**, 14504.