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# Reconsideration of the Ediacaran problematicum *Aulozoon*

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## ABSTRACT

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*Aulozoon scoliorum* is best known from a single large slab from the Nilpena Member of the Rawnsley Quartzite of South Australia, representing an Ediacaran paleocommunity, including *Phyllozoon hanseni*, *Dickinsonia costata*, *Aspidella terranovica, Pseudorhizostomites howchini,* and *Somatohelix sinuosus*. The source of this slab in Bathtub Gorge is the surface of a thick red sandstone with pseudomorphs of gypsum desert roses, which is interpreted as a Gypsid paleosol of the Muru pedotype. On this "snakes and ladders slab" (nicknamed for snake–like *Aulozoon* and ladder–like *Phyllozoon*), four specimens of *Dickinsonia* are poorly preserved above rounded terminations of *Aulozoon*. *Aulozoon* also has been discovered in five other thin sections cut below *Dickinsonia* basal surfaces, and in one case it is attached to *Dickinsonia*. *Aulozoon* has a high width to thickness ratio (14 ± 0.7), even after accounting for burial compaction. Burrows this much wider than high are unknown, and would be mechanically difficult for a burrower. Stronger objections to a burrow interpretation come from taper of *Aulozoon* to half its width, and local lateral crimping. Unlike deep sea tube worms, animal or algal stolons, *Aulozoon* is not cylindrical, and lacks a finished inside wall outline. Outer finished wall grading inwards to sandstone fill of *Aulozoon scoliorum* is most like a fungal rhizomorph with loose internal hyphae, and this biological interpretation is supported by growth within a paleosol with desert roses.

**Key–words**—*Aulozoon*, *Phyllozoon*, *Dickinsonia*, Vendobionta, Ediacaran.

## INTRODUCTION

*AULOZOON scoliorum* Gehling and Runnegar (2022) is a name for enigmatic fossils that are strap–like and sandstone–filled, on a stunning large fossil slab nicknamed "snakes and ladders" (after snake–like *Aulozoon* and ladder–like *Phyllozoon*) in a former display of the Ediacaran fossils in the South Australian Museum, Adelaide. *Aulozoon* is mainly known from the Nilpena Member of the Rawnsley Quartzite in the Flinders Ranges of South Australia (Fig. 1), but also has been found attached to *Dickinsonia* on slabs from Lyamtsa, in the White Sea region of Russia, in the Ediacaran Ust Pinega Formation (Ivantsov *et al*., 2019). The "snakes and ladders slab" also contains *Phyllozoon hanseni*, *Dickinsonia costata*, *Aspidella terranovica, Pseudorhizostomites howchini,* and *Somatohelix sinuosus* in a stunning life assemblage which reveals important new details about these enigmatic Ediacaran fossils (Gehling & Runnegar, 2022).

This contribution adds to previous descriptions of the "snakes and ladders slab" (Runnegar, 1994; Retallack, 2007; Gehling & Runnegar, 2022), but also details appearance of *Aulozoon* in petrographic thin sections and the microstratigraphy of its type locality. Biological affinities of *Aulozoon* remain unclear, with a range of plausible animal or fungal possibilities, and controversy, whether it is a trace or body fossil. Furthermore, *Aulozoon* is relevant to interpretation of closely associated *Dickinsonia*, which has been interpreted as a fungus or lichen (Retallack, 2007, 2020), xenophyophore foraminiferan (Seilacher *et al*., 2003), cnidarian (Harrington & Moore, 1956), worm (Wade, 1968; Runnegar, 1982), placozoan (Sperling & Vinther, 2010), animal (Bobrovskiy *et al*., 2018), or extinct stem eumetazoan (Evans *et al.,* 2019a, b).

## MATERIALS AND METHODS

This is a study of a large slab collected in Bathtub Gorge, central Flinders Ranges (Figs 1–3) by Jim Gehling and Bruce Runnegar in several pieces (South Australian Museum SAM P35665–86) during 1992 and 1994 (Gehling, 1999), and reassembled for display as the "snakes and ladders" slab (Figs 4–5). The locality was revisited by me in 2008 using

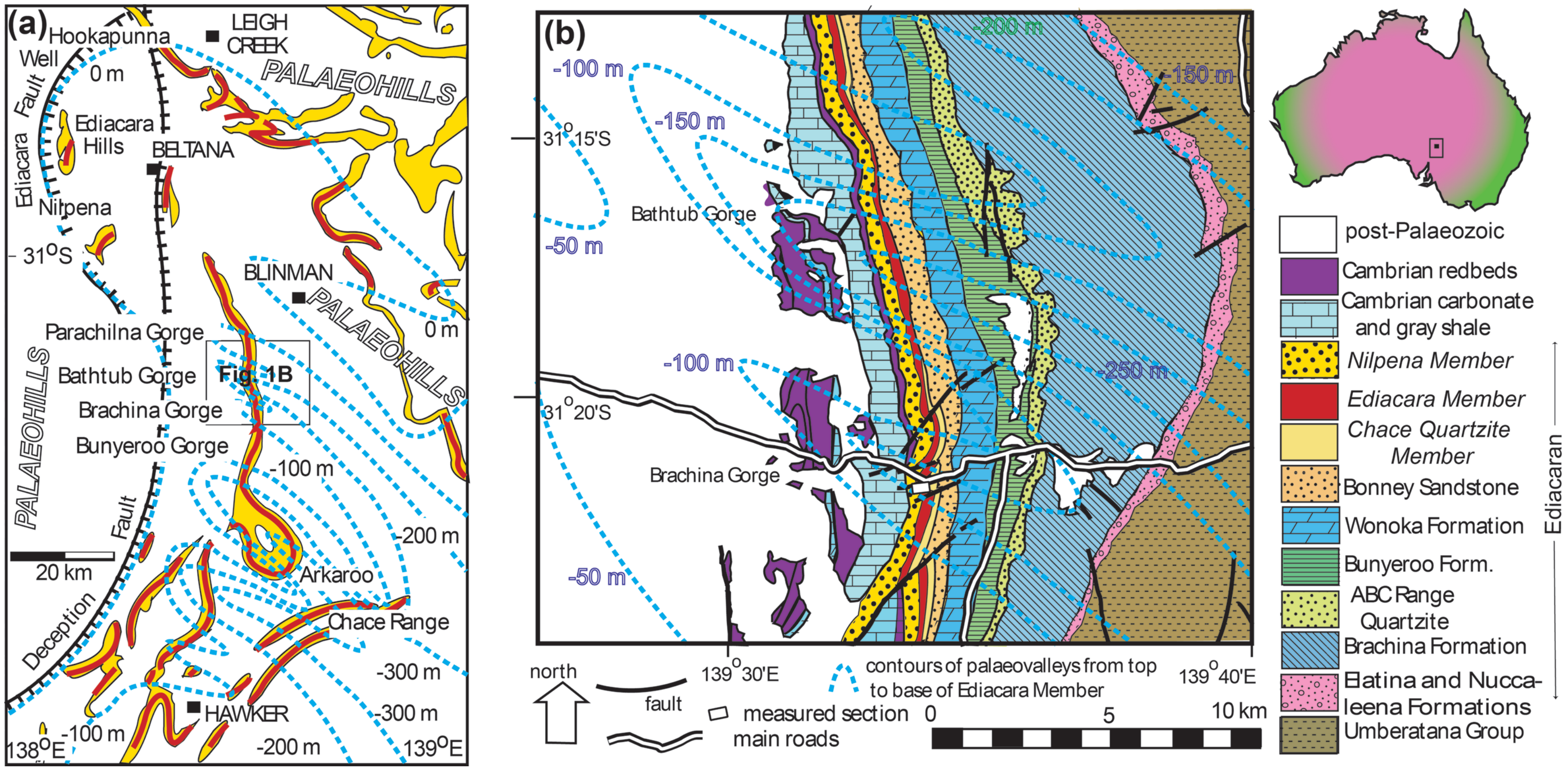

Fig. 1—Geological map of the Flinders Ranges (a) with detail of Bathtub and Brachina Gorges, South Australia (b). Contours on isopachs of the Ediacara Member as indications of paleotopography are from Gehling (2000).

coordinates and detailed directions from both Runnegar and Gehling, now published (Gehling & Runnegar, 2022). The gorge is a narrow (5 m) strike valley at this site, just east of the dry waterfall and a prominent bathtub–shaped waterhole (S31.245011°, E138.538350°). Cross sections of *Aulozoon* and *Phyllozoon* (Fig. 2a–b) were visible close to creek level, where a detailed measured section was prepared (Fig. 3). This measured section was 4 m along strike and closer to creek level than the collection site of the "snakes and ladders slab" detailed by Gehling and Runnegar (2022).

The slab was photographed and measured using digital calipers in the South Australian Museum. Oriented thin sections from other localities were also found with strap–like fossils of *Aulozoon* a few mm below or attached to the bottom of *Dickinsonia* in the same thin sections (Fig. 6a–b). These additional discoveries in thin section are simple sand–filled straps, lined with ferruginized organic matter, unlike more complex chambered, composite, or lobed structures in thin sections of *Aspidella*, *Funisia*, frond holdfasts, or *Dickinsonia* (Droser & Gehling, 2008; Tarhan *et al.*, 2016; Retallack, 2016b).

## GEOLOGICAL SETTING

*Aulozoon* and *Phyllozoon* are rare elements of the Ediacaran biota of the Flinders Ranges of South Australia, better known from iconic fossils such as *Dickinsonia* and *Spriggina* (Runnegar, 2022). These enigmatic soft–bodied fossils in sandstones of the Ediacaran Period represent a multicellular transition from microbial life of the earlier Precambrian to megascopic biota of the Paleozoic Era (Seilacher *et al.*, 2005; Buatois & Mángano, 2016).

The stratigraphic level of abundant *Aulozoon* and *Phyllozoon* over 10 m of outcrop in Bathtub Gorge (Fig. 2a–b), is within the Nilpena Member of the Rawnsley Quartzite of late Ediacaran age. This stratigraphic level can be correlated lithologically with basal Nilpena Member, where nodular sandstones also overlie a red silty interval, in the measured section in Brachina Gorge, 11 km to the south (Retallack, 2012a, 2013a), and dated at 547 ± 6 Ma using a poorly constrained age model of Retallack *et al.* (2014). Additional specimens of *Aulozoon* were found in thin sections of the Nilpena Member in Brachina Gorge (S31.34422° E138.55763°), and near Hookapunna Well (S30.58518° E138.30904°). *Aulozoon* has also been recorded from comparable, stratigraphic levels on Nilpena Station (Hall *et al.*, 2015; Reid *et al.*, 2018; Droser *et al.*, 2019), and in the Ediacara Hills (Glaessner, 1969). Thus, *Aulozoon* is widely distributed over 3000 km$^2$ from Hookapunna Well to the north (Retallack, 2016b), Ediacara Hills (Glaessner, 1969), Nilpena (Hall *et al.*, 2015; Reid *et al.*, 2018; Droser *et al.*, 2019) to the west, and Brachina Gorge (Retallack, 2016b) and Bathtub Gorge to the east (Gehling *et al.*, 2005; Retallack, 2013a).

The Hookapunna Well specimen was found loose on the surface, and so of uncertain stratigraphic level, but both the Brachina and Bathtub Gorge specimens were excavated from red cliff–forming sandstones with rounded nodules, of white, radiating sand crystals. Gehling (2000, p. 76) interpreted these as "sand rosettes" and "sand–gypsum crystals", and this was confirmed by their monoclinic selenite crystal form in thin section (Fig. 2b–d). These nodular sandstones below the "snakes and ladders slab" are also illustrated by Gehling and Runnegar (2022, fig. 4b). These beds with desert roses have been interpreted as paleosols of the Muru pedotype (Fig. 3), with *Aulozoon* and other fossils on the surface (A) horizon and sand crystals as a gypsic (By) horizon (Retallack, 2012a, 2013a). A v–shaped desiccation crack in this sandstone is an unusual feature illustrated elsewhere (Retallack, 2012a, fig. 8b), and best understood as desiccation of a microbial earth, so that sand acted like mud (Prave, 2002). The surface immediately above *Aulozoon* and *Phyllozoon* has "old elephant skin texture" of a microbial earth (Retallack, 2012a), and is not a laminated microbial mat.

From a sedimentary facies perspective, rocks with desert roses are in "Facies Association A, with common sand rosettes probably formed as upper intertidal sand flats" (Gehling, 2000), a paleoenvironment also envisaged by Jenkins *et al.* (1983). Facies A of Gehling (2000) was excluded from the Ediacara Member of Jenkins *et al.* (1983), and is now assigned to the basal Nilpena Member (Gehling & Runnegar, 2022). Such sand–rosette and nodular beds would be classified as Gypsids in soil taxonomy (Soil Survey Staff, 2014). The "supratidal facies with sand pseudomorphs after gypsum" was also illustrated by Gehling & Droser (2012), but later all South Australian Ediacaran facies became intertidal or deeper marine. Facies Association A became "shoreface sands" in the revised facies interpretation of Gehling & Droser (2013), and a "deeply subtidal matground" of Gehling and Runnegar (2022).

Desert roses do not form in permanently saturated marine environments, where gypsum and other evaporites form clear crystals by displacing clastic matrix (Warren, 2016). There are multiple other lines of evidence for this and other paleosols in the Rawnsley Quartzite of South Australia: mineral and grain size modal variation within beds (Retallack, 2012a), geochemical mass balance (tau) (Retallack, 2013a), $\delta^{18}O$–$\delta^{13}C$ correlation within carbonate nodules (Retallack, 2016a), low boron assay (Retallack, 2020), Ge–Si ratios of silica cement (Retallack, 2017), and eolian interbeds inferred from granulometry and sedimentary structures (Retallack, 2019; McMahon *et al.*, 2020). None of this evidence is addressed by recent research assuming the traditional view that these were marine fossils (Tarhan *et al.*, 2015, 2016; Evans *et al.*, 2019a, b, 2020; Gehling & Runnegar, 2022). Three recent studies assuming that they were benthic marine invertebrates do not uniquely support that interpretation: complex rank abundance distribution (Darroch *et al.*, 2018), very high β–diversity

Fig. 2—(a) Thin white lenses of edge of the *Aulozoon scoliorum* "snakes and ladders" horizon above a paleosol with silica–pseudomorphed gypsum desert roses (at arrows) in Bathtub Gorge, South Australia: (b) cross sections of *Phyllozoon* (left arrow) and *Aulozoon* (right arrow); (c) sections of gypsum desert–rose pseudomorphs in Muru paleosol in Brachina Gorge; (d) weathered out gypsum desert rose pseudomorphs at Arkaroo Rock; (e) petrographic thin section in plane light of desert rose pseudomorph in Inga paleosol in Brachina Gorge (Museum of Natural and Cultural History, University of Oregon specimen R3229).

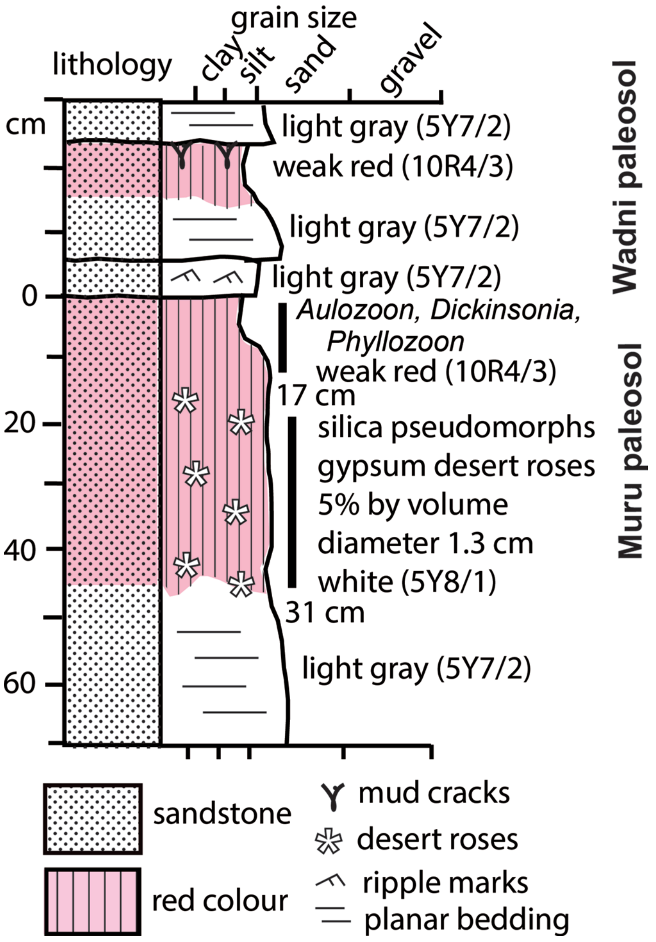

Fig. 3—Stratigraphic section through the Muru paleosol of the *Aulozoon* "snakes and ladders slab" in Bathtub Gorge, South Australia.

(Finnegan *et al*., 2019), and very low interspecific interactions (Mitchell & Butterfield, 2018). These three distinctive properties are characteristic of sessile communities of plants and lichens (Kuusinen, 1994; Dietrich & Scheidegger, 1997; Kessler *et al*., 2009; Thor *et al*., 2010; Fernandez–Going *et al*. 2013; Ulrich *et al*., 2016).

A detailed critique by Runnegar (2022) of the idea of paleosols associated with *Dickinsonia* (Retallack, 2012a, 2013a) is based on the following incorrect assertions: (1) lignin in *Dickinsonia*, (2) quartz sands have insufficient nutrition for terrestrial organisms, (3) Ediacaran paleosols do not have B horizons, (4) resistant fossils should resist sediment deformation, (5) red colour is Cenozoic not Ediacaran, (6) Newfoundland does not have Ediacaran paleosols, and (7) *Dickinsonia* is unlike a lichen. The rigidity of *Dickinsonia* was demonstrably more compaction resistant than wood and comparable with fossil fungi (Retallack, 1994), and likely due to fungal chitin rather than plant lignin (Retallack, 2007). Oligotrophic substrates are no more problematic for lush vegetative cover of plants and lichens (Retallack, 2022a), than for sparse animals in quartzose beaches and subtidal sands (Seilacher, 2007a). Ediacaran paleosols lack argillic horizons (Bt), which appeared with the Devonian evolution of tree roots (Retallack, 2022a), but have a variety of cambic (Bw), calcic (Bk), and gypsic (By) horizons (Retallack, 2012a, 2013a). *Dickinsonia* was deformed in Warrutu beds by sequential overlapping episodes of top–down melting of discontinuous permafrost, not by soft sediment deformation (Retallack, 2012a, 2013a). Ediacaran sediment oxidation is demonstrated by claystone breccias with both red and green clasts (McMahon *et al*., 2020), and boreholes into Ediacaran red beds below drab strata (Retallack, 2013a). Deep marine Ediacaran paleoenvironment of Newfoundland is falsified by matrix–supported accretionary lapilli and sanidine tuffs, which would have coarse grains at the base of the bed if deposited in water, as well as by a variety of geochemical proxies (Retallack, 2016a, 2020). Furthermore, the Ediacaran forearc basin of Newfoundland is on continental granitic basement, not deep–sea pillow basalts (Retallack, 2014). *Dickinsonia* looks like no animal (Seilacher, 1992), and its fractal system of isomers is similar to those of pseudomeristematic growth in crustose lichens (Retallack, 1994, 2007, 2022b).

## DESCRIPTION AND MEASUREMENTS

Ribbons of *Aulozoon* are smooth and featureless, without undulation, tessellation, segmentation, or regularity of sinuosity. These fossils have modest relief, enabling estimates of thickness as well as width (Figs 4–5), but thickness measurements presented here were from thin sections (Figs 6–7). A seam separating the ribbon from sediment in thin section may reflect decay and ferruginization of an organic sheath (Fig. 6a). A thin section showing an *Aulozoon* ribbon (Fig. 6a) was cut from a "footprint" (Evans *et al*., 2019a), or underside (Retallack, 2016b) of a small *Dickinsonia costata* illustrated in Fig. 5e.

There is substantial narrowing of width along the length, and also locally on tight turns like crimping of a hollow tube. On the "snakes and ladders slab" the ratio of width to thickness is 14 ± 0.7 (Fig. 7). Burial compaction of sandstones at this stratigraphic level has been calculated as about 60% of former thickness (Retallack, 2007), but recent determination of a Weaver index of illitization (10Å/10.5Å peak height) of 3.2 for *Dickinsonia costata* from Brachina Gorge (Retallack, 2020) gives burial depth of 3.47 km (using depth function of Retallack, 2013a) and compaction to 61.4% (using equation of Sheldon & Retallack, 2001). Correcting for compaction thus gives an original ratio of width to thickness of 9 ± 4: still much broader than thick.

The width of *Aulozoon scoliorum* is highly variable, tapering to half width on short segments. The average width of 245 measurements every 5 mm along each of the specimens

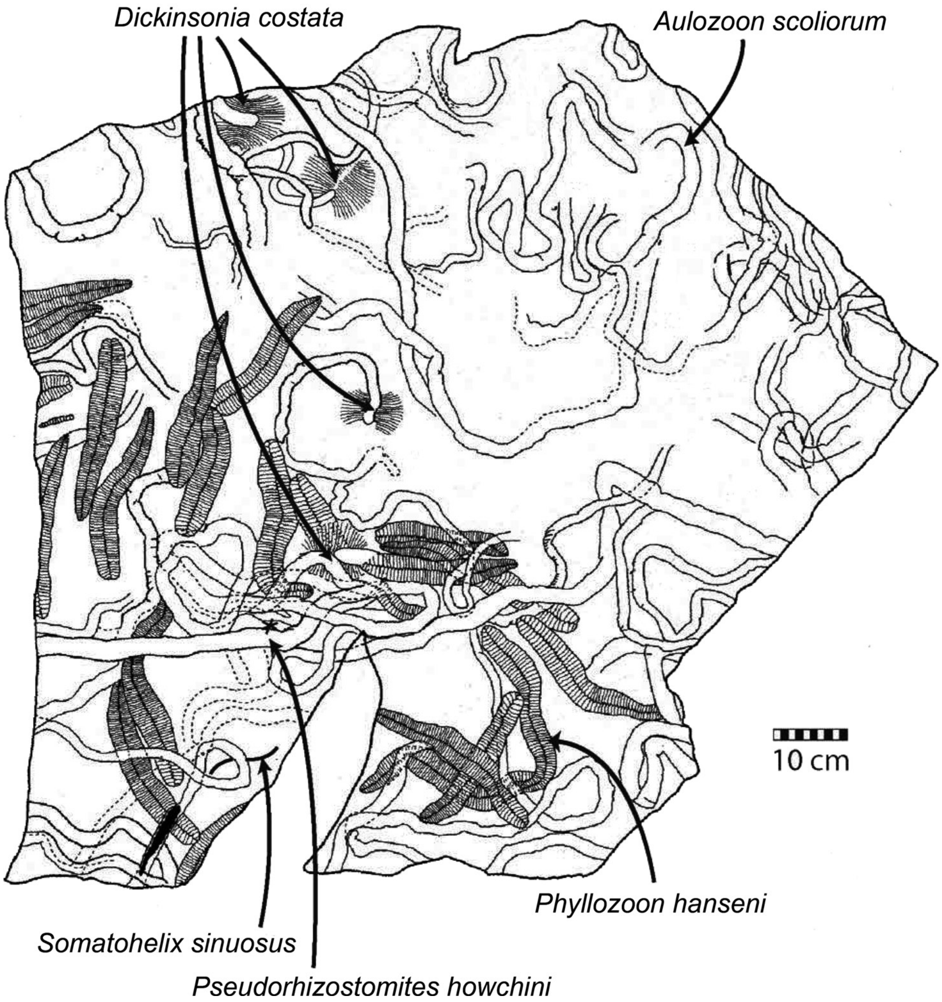

Fig. 4—Line drawing interpretation of the *Aulozoon* "snakes and ladders" slab (South Australian Museum P35665–86). Old elephant skin background texture has been omitted for clarity, but is captured in the comparable line drawing of Seilacher *et al.* (2003, 2005) and visible in Fig. 5.

on the "snakes and ladders" slab (SAM P35665–86) was 18.7 ± 5.4 mm (± 1 standard deviation). This distribution is right skewed and significantly different from a normal distribution for the same mean and standard deviation (solid line in Fig. 7a). Thickness of *Aulozoon* was best measured from thin sections of three specimens (F115735–6, F117737), and this also was variable at 1.3 ± 0.8 mm (22 measurements at 1 mm intervals), and also right skewed (Fig. 7b). Two cross sections of *Aulozoon* figured by Gehling & Runnegar (2022, fig. 10a, d) are unusually thick: 3 and 5 mm. Four of the *Aulozoon* ribbons on the "snakes and ladders slab" show a rounded termination, but none of them show a complete length. The longest one on the slab is 1.7 m long.

## TRACE OR BODY FOSSIL?

*Aulozooon* was at first considered a trace fossil (Glaessner, 1969; Jenkins, 1995; Seilacher *et al*., 2003), but later a body fossil (Runnegar, 1994; Retallack, 2007, Gehling *et al.*, 2005; Gehling & Runnegar, 2022). Adolf Seilacher (2007a, b; Seilacher & Gishlick 2014) continued to regard *Aulozoon* as a flatworm burrow, but called for experiments to demonstrate the possibility that a burrower ten times wider than thickness could burrow for meters under a few centimeters of sediment. Earlier, Glaessner (1969) and Jenkins (1995) had identified *Aulozoon* as the worm burrow *Palaeophycus* (Pemberton & Frey 1982), which has an ellipsoidal and less flattened outline allowing strong peristaltic burrowing motion.

Gehling *et al.* (2005) and Gehling and Runnegar (2022) considered the "snakes and ladder slab" a tangle of body fossils winnowed from its sedimentary matrix. Seilacher

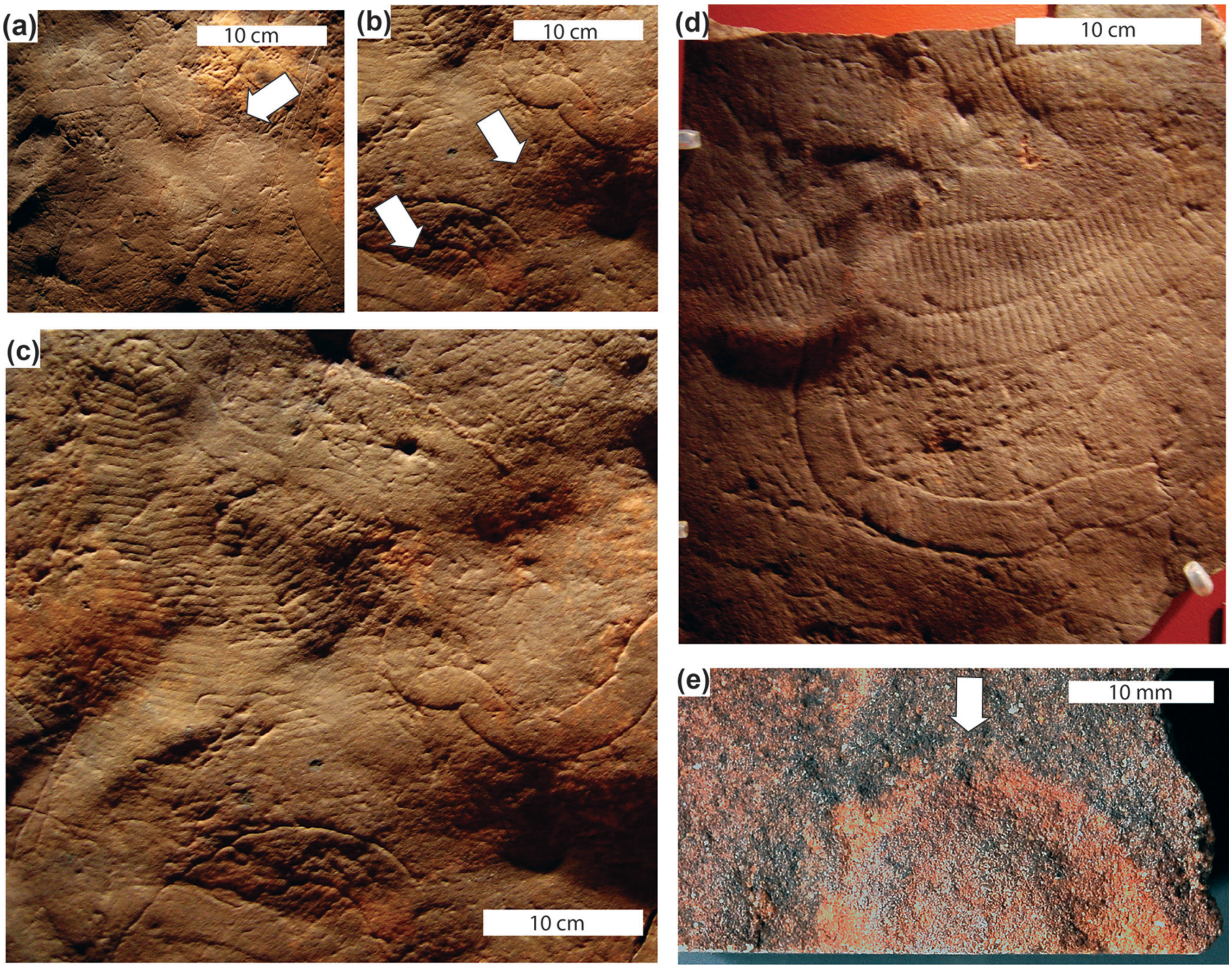

Fig. 5—*Aulozoon, Phyllozoon*, and *Dickinsonia* ghosts on the "snakes and ladders" slab (a–d) and underside of *Dickinsonia costata* (e) with *Aulozoon* revealed below it by thin section (Fig. 6a): Terminations of *Aulozoon* in faint *Dickinsonia* are indicated by arrows (a–b). Specimens are in the South Australian Museum (a–c are details of P35665–86 and d is P35690) and Condon Collection of the Museum of Natural and Cultural History University of Oregon (e is F115736).

(2007a) regarded this as unlikely because of preserved subsurface tiering, which is consistent over 2 m. A winnowed assemblage would have been rolled up like wracks of stranded seaweed. Furthermore, the orientation of *Phyllozoon* fossils is at 139.5° azimuth to current ripples on the upper surface of the slab (Gehling & Runnegar, 2022, fig. 5). My observations support the proposed 4 tiers of Seilacher (2007a) and Seilacher *et al.* (2003) within the 2 cm of relief preserved on the slab, here illustrated from the bottom (Figs 4–5). These tiers are (1) most *Aulozoon* (surface of upside–down slab so originally lowest), with *Somatohelix* and base of *Pseudorhizostomites*, (2) *Phyllozoon* and *Aspidella*, in some cases overlapping with *Aulozoon*, (3) old elephant skin (*Rivularites repertus*), and (4) poorly preserved (indistinct) *Dickinsonia* (deepest within upside–down slab and so originally at the top).

The chief problem with trace fossil interpretation of *Aulozoon* is local crimping and narrowing in width to half along the tube (Fig. 4). True burrows are constant in width of the burrowing organism (Seilacher, 2007a), One exception is slime mold trails growing by aggregation to a grex of social amoebae, such as *Lamonte*, but *Aulozoon* lacks backfills, levees or any other trace of slime–mold grex motion (Retallack, 2013b). Also notable is the way in which *Aulozoon* sometimes penetrates associated *Phyllozoon* (Gehling & Runnegar, 2022), but mostly sidles along, or passes over and under them (Figs 4, 5a–d), unlike trails with levees ploughing through immobile *Dickinsonia* (Gehling & Droser, 2018). Also odd are the tight and irregular turns, including one that appears to be a back flip (lower right in Fig. 4).

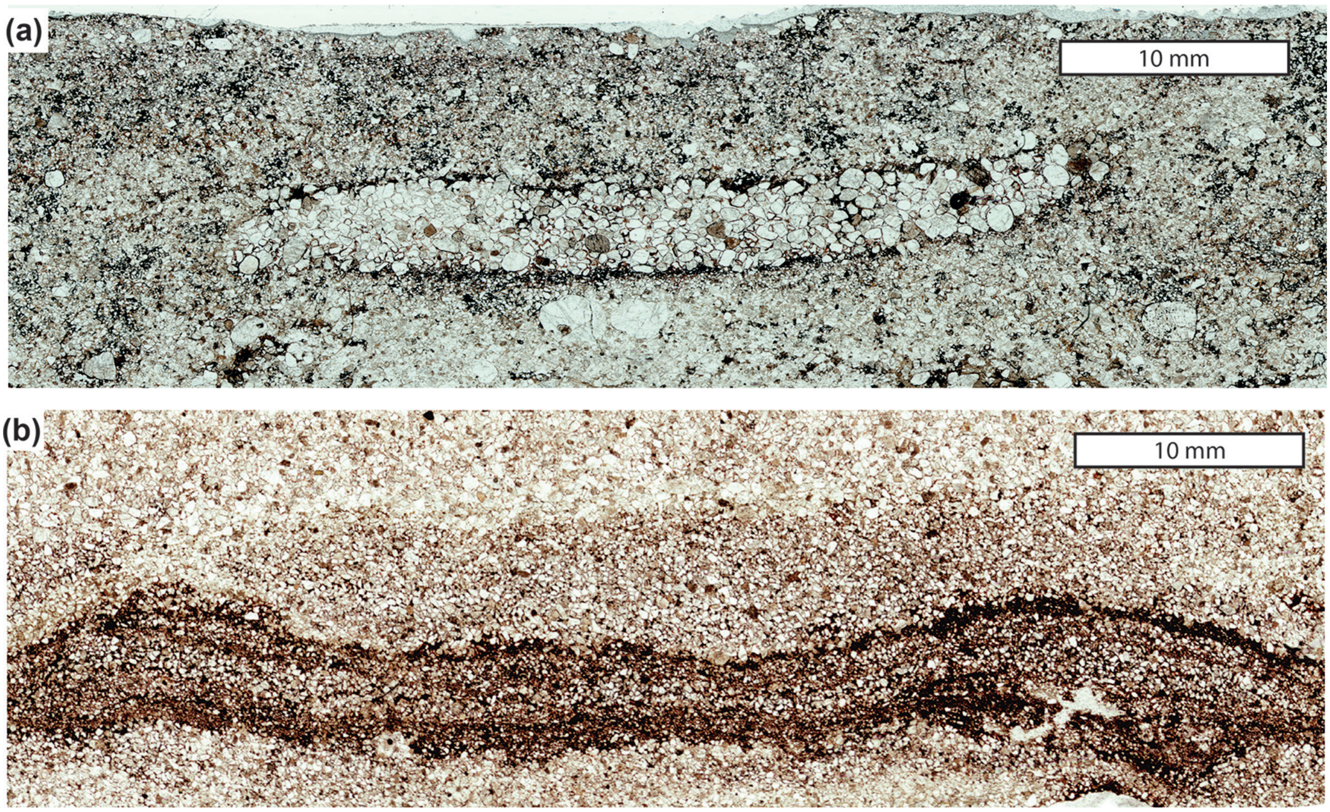

Fig. 6—*Aulozoon* in petrographic thin section below a *Dickinsonia* basal impression (a), and cross section of *Dickinsonia* with chamber partitions extending down into *Aulozoon* as if attached on the right side (b). Original top in these oriented thin sections is up. Condon Collection of the Museum of Natural and Cultural History University of Oregon (a is F117937, b is F115735) both from Muru paleosols in Brachina Gorge.

The question of body or trace fossil is also relevant to other fossils on the "snakes and ladders slab". Especially closely associated is *Dickinsonia costata*, because rounded terminations of *Aulozoon* are centered on the four specimens of *Dickinsonia* on the slab (Fig. 4), and one thin section shows septation of *Dickinsonia* continuing down into *Aulozoon* as if attached (lower right–hand side of Fig. 6b). Russian specimens regarded here as *Aulozoon* also are attached to one end of *Dickinsonia* (Ivantsov *et al*., 2019). *Dickinsonia* is best known as a negative hyporelief, concave on the overlying slab (Retallack, 2016b), but specimens like those on the "snakes and ladders slab" with subdued relief have been interpreted as "footprints", thus trace fossils of *Dickinsonia* (Evans *et al.*, 2019a, b; Gehling & Runnegar, 2022). These "footprints" of *Dickinsonia* have also been given the trace fossil name "*Epibaion*" (Ivantsov & Malakhovskaya, 2002; Gehling *et al*., 2005; Ivantsov, 2013; Buatois & Mángano, 2016), but are taphomorphs not new taxa (Retallack, 2021). These faint "footprints" preserve *Aulozoon* in matrix below *Dickinsonia* in South Australia (Seilacher *et al*., 2003; Gehling & Runnegar, 2022), but specimens from Russia enter the lower side of fully inflated hyporeliefs of *Dickinsonia* (Ivantsov *et al*., 2019). The majority of *Dickinsonia* specimens are impressions of its upper surface in overlying sediment (Retallack, 2007), and this explains why *Aulozoon* is so rare, but *Dickinsonia* is so common. The footprints also have less marked quilting and radiating fibrous texture, as in the specimens on the "snakes and ladders slab" (Fig. 5a–b), and another specimen (Fig. 5e) thin sectioned to reveal *Aulozoon* below (Fig. 6a). An alternative to the footprint interpretation is that these are decayed remnants (taphomorphs) or impressions of the underside of sessile *Dickinsonia* (Retallack, 2016b), which has different appearance in hand specimen (Fig. 5e), and in thin section than the upper side (Fig. 6b). The orientation of "*Epibaion*" or "footprints" in large rings or trails, which has been taken as evidence of travel (Sperling & Vinther, 2010; Evans *et al.*, 2019a, b), can also be explained as displacement and overlap by frost boils (Retallack, 2016b, 2021), or as wind–blown, defrosted polsters (Pérez, 1994, 2020; Hotaling *et al.*, 2020).

Also important to understanding *Aulozoon* is *Phyllozoon hanseni* on the same slab. *Phyllozoon* is generally below *Aulozoon*, but sometimes above, and rarely cut by *Aulozoon* (Gehling & Runnegar, 2022). *Phyllozoon* has long been

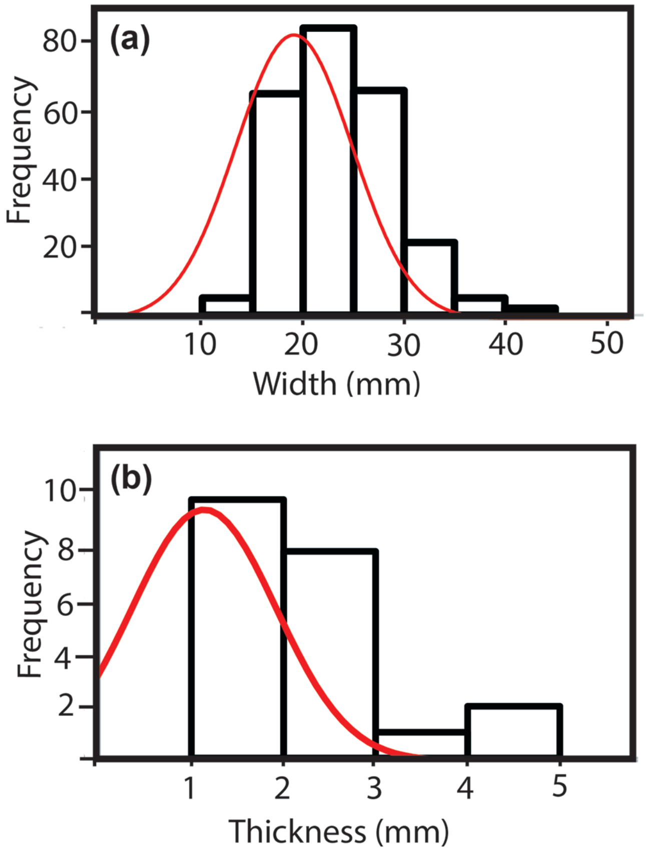

Fig. 7—Size distributions of *Aulozoon* width (a) and thickness (b). Red curves are computed normal distributions with the same mean and standard deviation as the histogram data.

considered a body fossil (Jenkins & Gehling 1978), perhaps buried in sediment to explain its preservation as a positive hyporelief (Seilacher 2007a). Gehling and Runnegar (2022) interpret *Phyllozoon* as a part of a matground, dead and buried, when *Aulozoon* grew around them. Retallack (2007) also noted general avoidance of *Phyllozoon* by *Aulozoo*n, and their comparable clarity of preservation, and suggested that *Phyllozoon* was a window lichen of the same community. There has been a suggestion that *Phyllozoon* is a trace fossil footprint (Ivantsov, 2013; Ivantsov & Malakhovskaya, 2002), but Evans *et al.* (2019a) argue against this for three reasons. First, the segmentation of *Phyllozoon* is more clearly and deeply defined than in specimens regarded as *Dickinsonia* "footprints". Second, *Phyllozoon* lacks clear anterior–posterior differentiation of animals. Third, *Phyllozoon* may be laterally linked in apparent fusion (Fig. 5d; Gehling & Runnegar, 2022, fig. 8), but does not overlap, again unlike specimens regarded as *Dickinsonia* footprints. Comparable underground intergrowth of adjacent individuals is also seen in other Ediacaran vendobionts, *Pteridinium* (Grazhdankin & Seilacher 2002), *Arumberia*, and *Ernietta* (Retallack & Broz, 2020).

*Aspidella terranovica* also has been found cutting across *Phyllozoon* at the same stratigraphic level in Bathtub Gorge as the "snakes and ladders slab" (Gehling & Retallack, 2022). The genus *Aspidella* has been widely misused as holdfasts of fronds (Tarhan *et al*., 2015; Reid *et al*., 2018), but this specimen has considerable relief and apical segmentation comparable with holotypic *Aspidella* from Newfoundland (Retallack, 2016b). *Aspidella* is a biconvex discoid fossil variously considered a cnidarian or vendobiont (Retallack & Broz, 2020).

A single specimen of *Pseudorhizostomites howchini* on the slab is a radiating set of grooves around a pit, which extend upward in this view of the lower surface of the slab. Originally envisaged as a body fossil of a cnidarian medusa (Sprigg 1949), *Pseudorhizostomites* was later interpreted as trace fossil, either a fluid escape structure of a decaying discoid (Glaessner & Wade, 1966; Wade, 1968), or a holdfast partially pulled out of the sediment by currents above (Tarhan *et al*., 2010, 2015). A more likely interpretation of *Pseudorhizostomites* is as a pseudofossil, a gas escape structure from a concentration of organic matter or microbes (Seilacher *et al*., 2003).

The upper surface of the slab between the various named fossils has a distinctive texture commonly called "old elephant skin", a complex set of intersecting fissures, pressure ridges, and pustules. This trace fossil of microbial consistence and deformation has been given the name *Rivularites repertus*, and interpreted as a microbial earth texture (Retallack, 2013a). It has also been interpreted as an aquatic microbial mat structure (Seilacher *et al*., 2003), but aquatic microbial mats are undulose like the trace fossil *Rugalichnus matthewi* (Stimson *et al*., 2017), and have internal lamination like stromatolites (Walter *et al*., 1979). When disrupted by fish or livestock, aquatic mats show rollups and dislodged flakes (Noffke *et al*., 2019), but not the multiple, highly deviatoric, extensional and compressional deformations of *Rivularites* well described by its common name of "old elephant skin".

Finally, a curved groove on the "snakes and ladders" slab was identified as a worm trail by (Seilacher *et al.* 2003; Seilacher 2007a, b; Seilacher & Gishlick, 2014). It is not a laterally leveed tube similar to trace fossils *Archaeonassa*, *Helminthopsis*, or *Helminthoidichnites* (Buatois & Mángano, 2016; Evans *et al*., 2020), nor crenellated like the enigmatic body fossil *Plexus ricei* (Joel *et al*., 2014). It is most like the body fossil *Somatohelix sinuosus* (Sappenfield *et al*., 2011). Thus, all the megafossils on the "snakes and ladders slab" are here interpreted as body fossils, not trace fossils.

Supposed scratch marks of "*Kimberichnus teruzzi*" disrupting *Phyllozoon hanseni* on the "snakes and ladders slab" are not accepted here, because the illustrations are acicular rods rather than open furrows (Gehling & Runnegar, 2022, fig. S3). These are more likely casts of needle ice

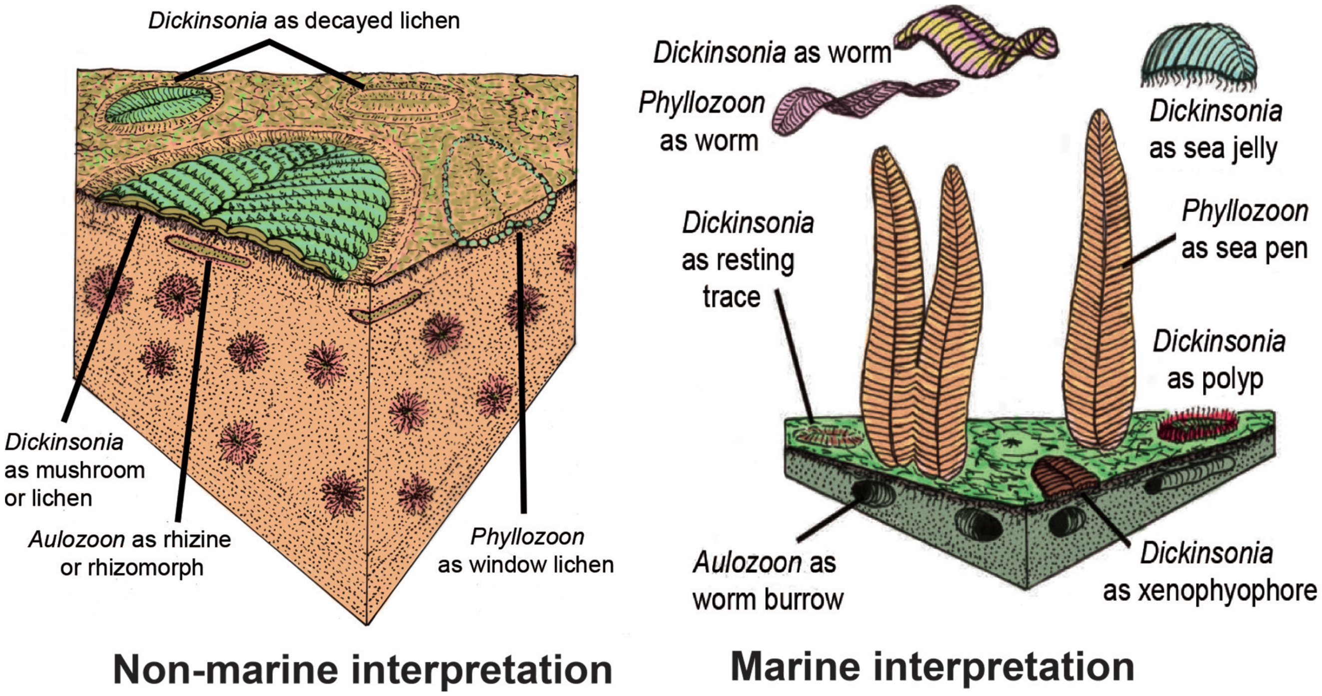

Fig. 8—Alternative biological interpretations of *Aulozoon*, *Phyllozoon*, and *Dickinsonia*.

(Retallack, 2021), but these short examples may also have been acicular crystals of thenardite ($Na_2SO_4$) or mirabilite ($Na_2SO_4 \cdot 10H_2O$), known in other Neoproterozoic rocks of South Australia (Retallack *et al.*, 2015).

## BIOLOGICAL INTERPRETATIONS OF *AULOZOON*

### Animal burrow or trail

Although *Aulozoon* has been regarded as a flatworm or placozoan burrow (Seilacher *et al.*, 2003), its high width–to–thickness ratio is unlike any known animal burrows, and there are doubts that what are today thin and flimsy creatures had the strength to move sediment even at such shallow depth (Seilacher & Gishlick, 2014). Nor is it a surface trail that was buried, as both the type material on the "snakes and ladders slab" (Figs 4–5) and specimens in thin section (Fig. 6) show that it was a three–dimensional structure with a ferruginized organic margin on top, sides, and bottom (Gehling & Runnegar, 2022). No levees, backfills or undulations of peristaltic motion are apparent, and the fill is coarser in grain size with rounder grains than those of the matrix (Fig. 6a). The most fatal objections to the animal burrow interpretation of *Aulozoon* are observed narrowing of the tube to half width and local crimping at bends like a sausage casing (Fig. 4). Ivantsov *et al*. (2019) propose that *Aulozoon* attached to one end of *Dickinsoni*a was its trail, but the trail is only a tenth of the width of *Dickinsonia* unlike other proposed intermittent trails of *Dickinsonia* (Evans *et al*., 2019a). Crisp burrows and trails also would be unlikely in the dry microbial earth of a desert soil (Fig. 8). *Aulozoon* was probably not an animal burrow or trail.

### Tube worm

Runnegar (1994) and Gehling & Runnegar (2022) compared *Aulozoon* on the "snakes and ladders slab" with vestimentiferan pogonophorans, like giant tube worms *Riftia pachyptila* (Jones, 1981). These bizarre creatures of deep–sea hydrothermal vents and cold seeps have chitinous tubes and lack a digestive tract, feeding instead from chemoautotrophic bacteria within an internal organ, the trophosome (Bright & Lallier, 2010). Pogonophoran tubes differ from *Aulozoon* in being cylindrical and often segmented (Jones, 1981; Bright & Lallier, 2010). In thin section there is a strong asymmetry of the wall of *Aulozoon* from smooth and finished on the outside, but grading inward to fill unlike sharpy delimited inside and outside of tubeworm walls. A vent or seep ecology is also unlikely for *Aulozoon* within a narrow interval of unveined sedimentary rock, and a soil with desert roses (Figs 3–6). *Aulozoon* was probably not a tube worm.

### Slime mold burrow

Tapering along the length of the Ediacaran burrows is known in *Lamonte trevallis* from the Dengying Formation of China (Chen *et al*., 2013; Meyer *et al*., 2014), and this unusual feature is understandable if the trace maker were a social amoeba or slime mold (Retallack, 2013b; Retallack & Mao, 2019). Living *Dictyostelium* (Mycetozoa) lives as dispersed amoebae in soil, but when food becomes scarce, amoebae aggregate to form a multicellular grex ("slug"), which moves across or through the soil a short distance, widening with newly recruited amoebae, until it forms a mound from which a stalk grows upward to release spores (Bonner, 2009). Likely examples of widening slime mold burrows and trails in the fossil record (Chen *et al.*, 2013; Retallack, 2013b; Meyer *et al.*, 2014; Retallack & Mao, 2019; El Albani *et al.*, 2019) show a variety of features not seen in *Aulozoon*: short lengths of only 5–10 cm between narrow inception and swollen termination, arcuate marks of movement, and lateral levees. *Aulozoon* was probably not a slime mold burrow.

### Stolon

Was *Aulozoon* a stolon of *Dickinsonia* considered as a colonial animal or modular plant? Stolons are known in hydroids (Overton, 1963; Blackstone & Buss, 1991), algae (Hayee–Memon & Shameel, 1996; Komatsu *et al.*, 1997), and vascular plants (Mathew *et al.*, 1989; Waters & Watson, 2015)? Poorly preserved *Dickinsonia* at the ends of four *Aulozoon* tubes would thus be like hydroid polyps and recall past interpretation of *Dickinsonia* as a cnidarian (Harrington & Moore, 1956). Red algal affinities for vendobionts have also been suggested before (Ford 1958). Stolon–like connections between Ediacaran fossils including *Charniodiscus* described by Liu and Dunn (2020) are narrow, branching, and drab–haloed, unlike *Aulozoon*, and can be identified as *Prasinema* (Retallack, 2011), a controversial ichnogenus (Jago *et al.*, 2012; Retallack, 2012b). Land plant affinities are not likely for any Ediacaran fossils, but there is evidence from spores for non–vascular land plants as old as Cambrian (Strother, 2016). Stolons are tubular with finished inside and outside surfaces of the walls, rather than flattened with graded walls like *Aulozoon*. Stolons also show branches to individual units, and holdfasts, not seen in *Aulozoon*.

Interpretation as a stolon to *Dickinsonia* would imply that *Dickinsonia* was an animal or alga, both compatible with discovery of cholestanes ($C^{27}$) as remnants of cholesterol in fossil *Dickinsonia*, and also widespread in animals (Bobrovskiy *et al.*, 2018), and red algae (Rhodophyta: Chardon–Loriaux *et al.*, 1976). However, $C^{27}$ cholesterol is also common in many groups of fungi including Ascomycota (Kaneshiro & Wyder, 2000), Glomeromycota (Weete *et al.*, 2010; Grandmougin–Ferjani *et al.*, 1999), Zygomycota (Weete & Gandhi, 1997), and Chytridiomycota (Weete *et al.*, 1989). This phylogenetic distribution suggests that cholesterol is basal to fungi and algae, and ergosterol ($C^{28}$) evolved later (Weete *et al.*, 1989; Gold, 2018).

The stolon interpretation would also be countered by evidence of motile *Dickinsonia* from "intermittent trails" ("*Epibaion"*) of *Dickinsonia* (Ivantsov & Malakhovskaya, 2002; Ivantsov, 2013; Evans *et al*. 2019a, b), but these may instead be sessile individuals displaced by frost boils (Retallack, 2016a, 2021). Another periglacial alternative for so called "footprints" of *Dickinsonia* (Evans *et al*., 2019a) is as "errant lichens" or "glacier mice", which are wind–blown polsters gliding on melting ice (Pérez, 1994, 2020; Hotaling *et al*., 2020). Other periglacial features of the Ediacara Member in South Australia include permafrost convolutions (Retallack, 2012a), needle ice (Retallack, 2016a, 2021), and cold temperate paleotemperature from alumina/silica ratios (Retallack, 2013a). *Dickinsonia* was probably not a motile animal or stoloniferous animal or algal colony.

### Animal or fungal parasite, scavenger, or herbivore

If *Aulozoon* is not a burrow nor stolon, perhaps it was a non–colonial, sessile animal, or fungus in some way exploiting *Dickinsonia* to which it was attached? Scavenging of *Dickinsonia costata* has been interpreted from invasion of the trace fossil *Helminthoidichnites tenuis* (Gehling & Droser, 2018), now considered the trail of a small animal *Ikaria wariootia* (Evans *et al*., 2020). These partially eaten specimens of *Dickinsonia* have been considered scavenged and buried corpses, because if they were animals they would have moved away (Gehling & Droser, 2018). However, levees to *Helminthoidichnites* are evidence that these were not burrows but surface trails (Buatois & Mángano, 2016), and the partly consumed *Dickinsonia* specimens are crisp, undecayed, and show no evidence of avoidance (Retallack, 2007). This is more likely a case of herbivory or carnivory of sessile *Dickinsonia*, depending on one's vegetable or animal view of *Dickinsonia* (Bobrovskiy *et al*., 2019; Retallack, 2020). Comprehensive survey of Ediacaran slabs shows that such interaction between fossils is extremely rare, more like vegetation than Phanerozoic benthic marine communities (Mitchell & Butterfield, 2018; Mitchell *et al*., 2020). *Helminthoidichnites* is not known from the "snakes and ladders slab", but the body fossil recognized here as *Somatohelix* (Sappenfield *et al*., 2011) was once considered a "worm trail" like *Helminthoidichnites* (Seilacher *et al*., 2003). *Dickinsonia* on the "snakes and ladders slab" is poorly preserved, deflated, and partly decayed, but not consumed (Seilacher *et al*., 2003, 2005). The possible connection of *Aulozoon* and *Dickinsonia* shows apparent continuity of structure (Fig. 6b), and no clear reaction tissue, scar, or callus, resisting attack. Furthermore, *Aulozoon* is more abundant than *Dickinsonia* in a low productivity desert soil, and unlikely to have been parasite, scavenger, or herbivore.

### Fungal cord, rhizine or rhizomorph

If *Aulozoon* were not a separate organism, eating or parasitizing *Dickinsonia*, perhaps it was an underground part of *Dickinsonia* like a fungal cord, rhizome or rhizomorph. Comparable mycelial rhizomorphs include modern bootlace fungi (*Armillaria* spp: Basidiomycota: Mihail & Bruhn, 2005; Lamour *et al*., 2007), cord–forming fungi (*Pisolithus, Rhizopogon, Hypholoma*: Basidiomycota; Dowson *et al*., 1986; Allen, 2007; Simard, 2018), mycorrhizal threads (*Rhizophagus irregularis*, Glomeromycota: Olsson *et al*., 2014), and lichen rhizines (*Xanthoparmelia*, Ascomycota; Paradise, 1997; *Anzia*, Ascomycota, Liang *et al*., 2012). Rhizomorphs can be up to 5 mm wide and formed of thick–walled hyphae, densely packed into an exterior sheath, but loosely packed in the interior (Motta, 1969; Ott *et al*., 1993; Sanders & Ascaso, 1997; Ascaso & Wierchos, 1995; Yafetto, 2018). Fungal cord is a good match for the finished outer but gradational inner surface of the wall of *Aulozoon* in thin section (Fig. 6a), and its soil setting.

The Silurian fossil *Tortotubus* (Smith, 2016) was a cord–forming fungus originally identified as basidiomycotan, but more plausibly glomeromycotan or mucoromycotinan (Auxier *et al*., 2016). Drab–haloed, branching filaments referable to the ichnogenus *Prasinema* (Retallack, 2011) comparable with mycorrhizal networks are widespread in Ediacaran paleosols (Retallack, 2012a, 2013a, 2016a), and observed attached to fossils such as *Charniodiscus*, *Charnia*, *Primocandelabrum*, and *Heimalora* (Liu & Dunn, 2020). The enigmatic Ediacaran tubular fossils *Somatohelix* (Sappenfield *et al*., 2011), *Plexus* (Joel *et al*., 2014), and *Funisia* (Droser & Gehling 2008), are also plausible fungal cords or rhizomorphs, and if so would have been parallel to the surface rather than vertical to the surface as reconstructed (by Droser & Gehling, 2008; Sappenfield *et al*., 2011; Joel *et al*., 2014). Fungal cords, rhizomes or rhizomorphs branch more copiously than *Aulozoon*, but branching is greatly pruned by isopod herbivory (Crowther *et al*., 2013). Although a burrow was identified in association with *Aulozoon* by Seilacher *et al.* (2003, 2005), on close examination, this specimen is more like the body fossil *Somatohelix* (Sappenfield *et al*., 2011). There is a likely Ediacaran animal (*Ikaria*) within leveed trails (*Helminthoidichnites*: Evans *et al*., 2020) in the Nilpena Member of South Australia. Herbivore trimming may explain the lack of branching in *Aulozoon*, as a fungal rhizomorph.

## CONCLUSIONS

*Aulozoon scoliorum* is yet another enigmatic Ediacaran fossil: a strap–like, sand–filled organic tube 7–30 mm wide and 1–5 mm thick, closely associated on one large slab with *Dickinsonia costata*, *Phyllozoon hanseni*, *Aspidella terranovica*, *Somatohelix sinuosus*, *Pseudorhizostomites howchini* and *Rivularites repertus*. This "snakes and ladders slab" preserves a paleocommunity of the upper 2 cm of a red sandstone with silica pseudomorphs of gypsum desert roses, interpreted here as a semiarid Muru paleosol (of Retallack, 2013a), but as "shoreface sands" by Gehling & Droser (2013), and "deeply subtidal matground" by Gehling & Runnegar (2022). Five separate biological explanations for *Aulozoon* are considered: (1) flatworm burrow, (2) tube worm, (3) stolon of colonial animal or alga; (4) animal or fungal parasite, scavenger or herbivore, and (5) fungal cord, rhizomorph or rhizine. This last explanation is most consistent with its overall tapering and high width to height ratio, thin section micromorphology, and paleosol setting.

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