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Paleoecology of *Tribrachidium*: New Data From the Ediacaran of South Australia

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

Geological Sciences

by

Christine Meriwether Solon Hall

March 2015

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The Thesis of Christine Meriwether Solon Hall is approved:

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ABSTRACT OF THE THESIS

Paleoecology of *Tribrachidium*: New Data From the Ediacaran of South Australia

by

Christine Meriwether Solon Hall

Master of Science, Graduate Program in Geological Sciences

University of California, Riverside, March 2015

Dr. Mary L. Droser, Chairperson

Tribrachidium is a monospecific genus of the Ediacara biota that is found globally. In the Flinders Ranges of South Australia, the spatial distribution of *Tribrachidium* across the seafloor is best described as patchy. Although *Tribrachidium* is the dominant fossil on two of the twenty-six beds currently excavated and is present in large numbers on another, the genus most commonly occurs as no more than a handful of specimens on a bed. *Tribrachidium* size frequency distributions of each of the three beds with more than 5 specimens are all statistically distinguishable from one another. Additionally, the size range on any given bed is smaller than the overall size range observed for the genus. These patterns suggest that these organisms lived in populations composed of cohorts. The beds with numerous *Tribrachidium* come from different facies and are characterized by the presence of dissimilar mixes of taxa and textured organic surfaces, indicating that *Tribrachidium* was a generalist, able to adapt to a variety environments. Uniquely, the base or internal structure of *Tribrachidium* is also found preserved in both positive and negative relief as a sequence of concentric ridges on beds where *Tribrachidium* is the

dominant genus. The most parsimonious explanation for the presence of these concentric ridge fossils is that they are the fossilized form of a *Tribrachidium* preserved when the organism was buried upside-down, flipped over, or partially decayed prior to burial.

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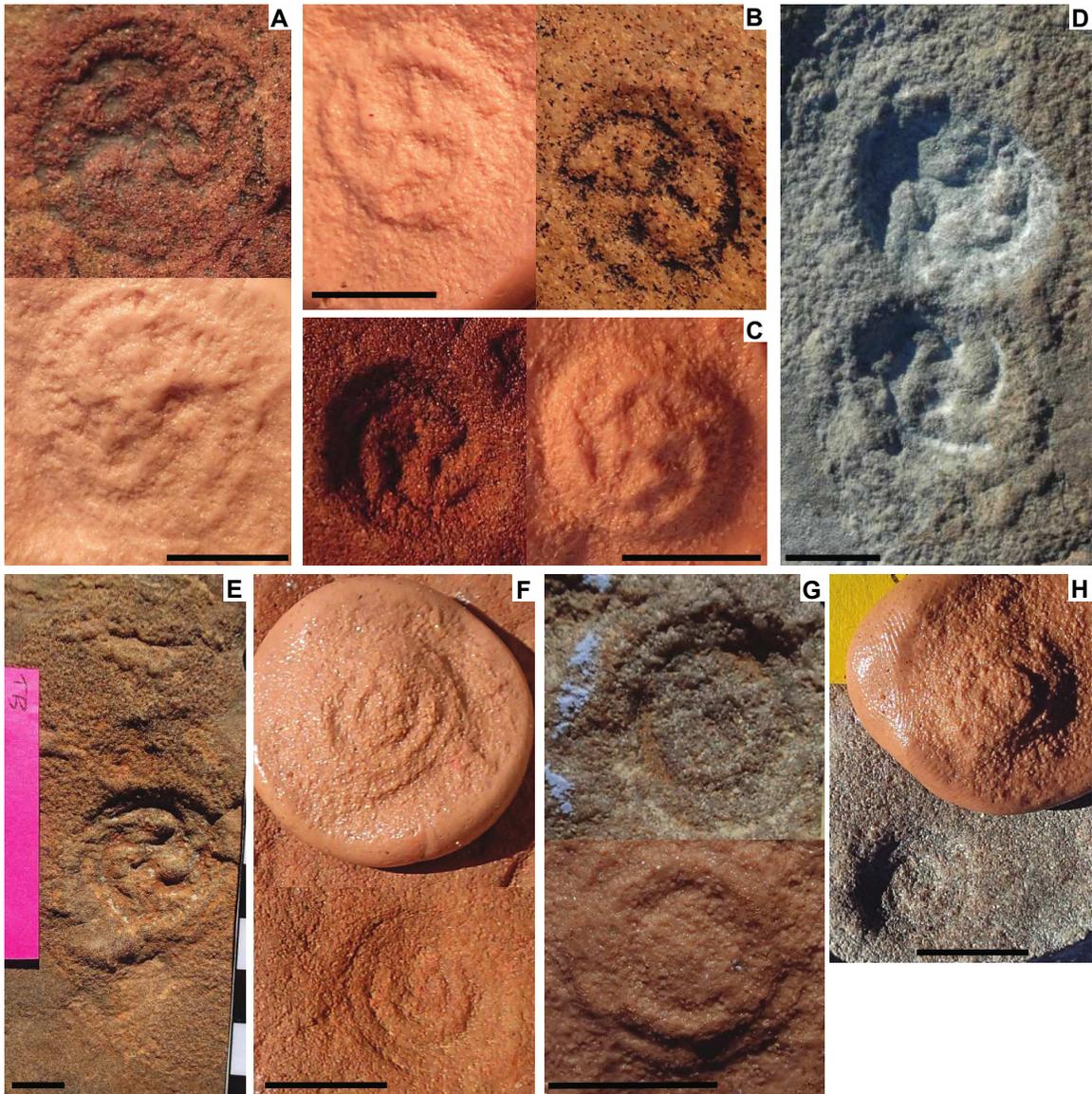
INTRODUCTION

The Ediacara biota includes a suite of globally distributed exceptionally-preserved, soft-bodied organisms that span the late Ediacaran Period from 575 million years ago to the end of the Precambrian (Narbonne, 2005; Xiao and Laflamme, 2009). Currently, there are about 50 described genera (Laflamme et al., 2013) that vary widely in size, from millimeters to over a meter, and also in shape and morphology (Narbonne, 2005). The Ediacara Member of the Rawnsley Quartzite, cropping out in the Flinders Ranges of South Australia is host to a diverse array of taxa that comprises a wide variety of morphologies (e.g. Droser and Gehling, in press). In South Australia, fossils of the Ediacara biota are also associated with a variety of textured organic surfaces (TOS), which consist of organic mats, fibers, and simple body fossils (Gehling and Droser, 2009), and have been preserved in a number of different facies (Gehling and Droser, 2013).

Tribrachidium heraldicum (Fig. 1A-C) is described as being nearly circular in shape with tri-radial symmetry, up to 2-3 cm in diameter, and can be distinguished by three ridges that radiate from the center and bend 90° in a clockwise direction. Well-preserved specimens also have numerous finer ridges, or a ‘tentacular fringe’, that extends from the bend in the arms to the edge of the specimen (Glaessner and Daily, 1959). In large specimens, this fringe or “caul” extends across the entire surface of the organism (Jenkins, 1992). A Y-shaped groove at the center interpreted as a mouth (Glaessner and

Wade, 1966), has not been confirmed in studies of hundreds of specimens. The slightly convex “bulla” found at the bend in each of the arms has been interpreted as a possible gonad or reproductive structure (Jenkins, 1992). Specimens collected in the Chace Range, 50 km southeast of Nilpena are more conical, with a height/diameter less than or equal to 0.5, depending on the sedimentary facies in which they are preserved (see Gehling, 1999). Like most genera of the Ediacara biota, *Tribrachidium* is monospecific (Laflamme et al., 2013). The taxonomic affinities of *Tribrachidium* are uncertain (Glaessner and Wade, 1966), but possible relationships to echinoderms (Paul, 1979), sponges (Seilacher, 1999; Narbonne, 2005), and cnidarians (Fedonkin and Cope, 1985; Valentine, 1992) have been suggested. Most recently, *Tribrachidium* has been linked to other tri-radial Ediacara taxa in a group called triradialomorphs (Laflamme et al., 2013). *Tribrachidium* was originally described from South Australia but is also found off the White Sea coast of Russia (Martin et al., 2000; Laflamme et al., 2013). Here we present new data on the population dynamics and environmental ecology of *Tribrachidium* that constrain its biology and ecological niche.

Figure 1. *Tribrachidium* specimens. *Tribrachidium* is preserved in negative relief on the base of beds. Where present, the silly putty molds show the organism as it would have looked sitting on the seafloor. All scale bars are 1 cm. A) *Tribrachidium heraldicum*. Note the tentacular fringe around the periphery of the organism. B-C) *Tribrachidium heraldicum*. D) An example of touching *Tribrachidium*. E) A *Tribrachidium* from TBEW in association with micropucker. F) Concentric ridge fossil from 1TT. G) A ‘stacked’ concentric ridge fossil, where the center ridge has higher relief than the edge. H) A ‘nestled’ concentric ridge fossil, where the relief is the same at the center as at the edge.



GEOLOGIC SETTING

The fossiliferous Ediacara Member of the Rawnsley Quartzite varying from 5-300 m in thickness, crops out in and near the Flinders Ranges, South Australia (Fig. 2) and occurs 200-600 m below a basal Cambrian disconformity (Gehling, 2000). The Ediacara Member is comprised of at least five distinct facies (Fig. 3): 1) shoreface sands: sandstone beds representing deposition at fair-weather wave base; 2) wave-base sands: thin-bedded, rippled sandstones representing deposition in shallow marine settings; 3) delta-front sands: poorly sorted, laminated silty sandstones representing deposition below wave base; 4) sheet-flow sands: laterally continuous event beds characterized by planar lamination and tool marks; and 5) mass-flow sands: very thick to massive slumped sandstones comprising the canyon fill (Gehling and Droser, 2013). At the National Heritage Ediacara fossil site at Nilpena Station, successive bedding planes multiple square meters in size have been excavated and analyzed. Fossils are typically preserved as molds on the base of beds.

Figure 2. A map of the field area in South Australia modified from Droser and Gehling (2008).

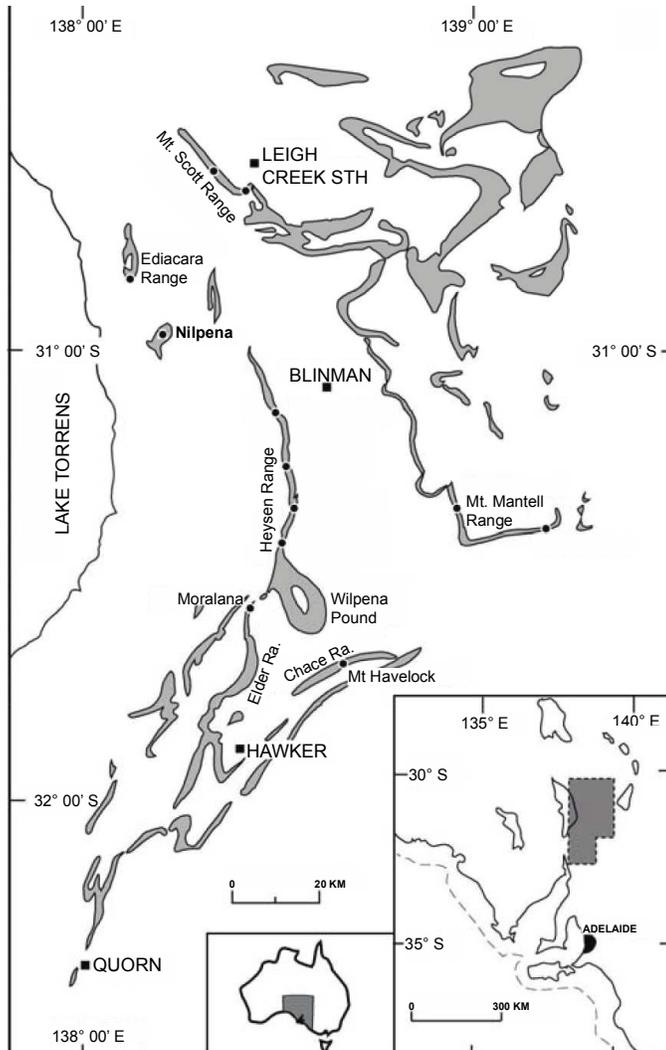
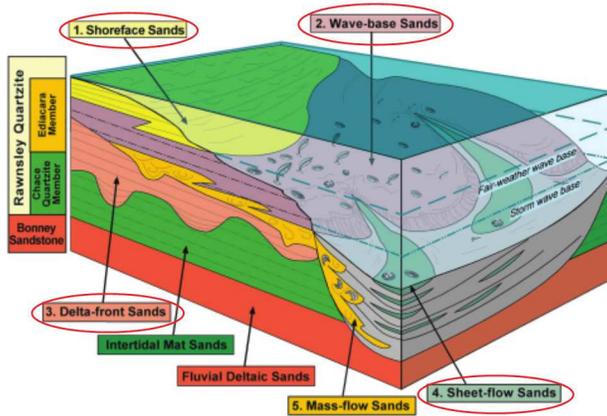


Figure 3. A diagram showing the described facies in which Ediacaran fossils occur at South Australia. Facies where *Tribrachidium* have been observed are circled. Modified from Gehling and Droser (2013).



METHODS

To date, 26 fossiliferous beds comprising more than 300 square meters of Ediacaran-aged seafloor have been excavated at Nilpena. Because the fossils are preserved on the bases of the beds, the beds are inverted during excavation to expose their bases before they are reassembled. The beds are then marked into square meter grids, and the locations of fossils are recorded with respect to the grid to create a record of the species, abundance, and spatial distribution of the individuals on the bed.

Latex molds were made of all of the *Tribrachidium* on the beds at Nilpena. Additionally, all known float specimens of *Tribrachidium*, as well as all of those specimens housed at the South Australia Museum, were also photographed and measured. The diameter of each fossil was measured from the latex using digital calipers. Partial specimens were

only used when more than half of the organism was preserved. Specimens found on the excavated beds have been left in place to enable further bed-scale research at the site.

RESULTS

Preservation and Morphological Variation

Tribrachidium occurs as the classic form with tentacular fringe typically in larger (>15 mm) specimens and rarely observed in smaller specimens, or those where the grainsize of external molds was more than 0.25 mm. In most of the specimens with a diameter <15 mm, the surface between the outer bend of the arm and the edge of the fossil is smooth.

There is a weak correlation between the distance from the center of the specimen to the bend in the arm and the distance from the bend in the arm to the edge of the organism (Fig. 4). The distance from the center to the arm bend is larger and seems to have continued growing while the growth of the outer edge slowed. Thus, the organism overall grew isometrically but internally, it grew allometrically. Generally speaking there is very little vertical relief observed in these fossils, but the height of *Tribrachidium* is loosely correlated to the diameter of the organism. Larger organisms tend to have more relief (Fig. 5), but the range of heights recorded at Nilpena is only about 2 mm. The slight increase in height also results in a marginally more conical shape. Although compaction during burial would have likely reduced the vertical relief (Gehling, 1999), the only evidence of deformation is minimal distortion of the edges in some specimens resulting in an overall sub-circular or slightly oval shape.

Figure 4. A graph of the distances from the center of the specimens to the bend in the arms vs. the distances from the arm bends to the edge of the organisms for the *Tribrachidium* at Nilpena. In the inset, (A) shows an example distance from the center to the arm bend, and (B) shows an example distance from the arm bend to the edge of the specimen. The distance from the center to the arm bend is larger, and likely continued to grow even as the growth of the outer edge slowed.

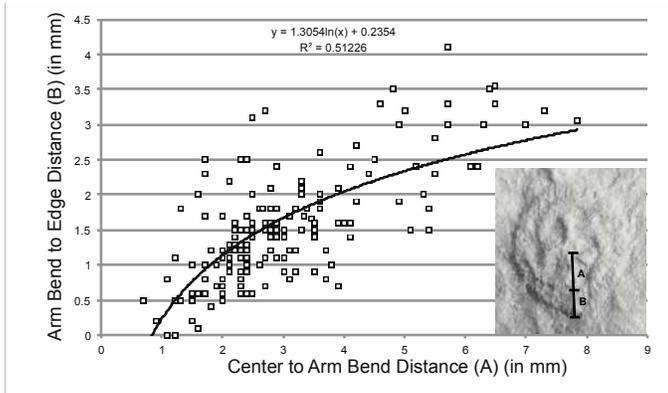
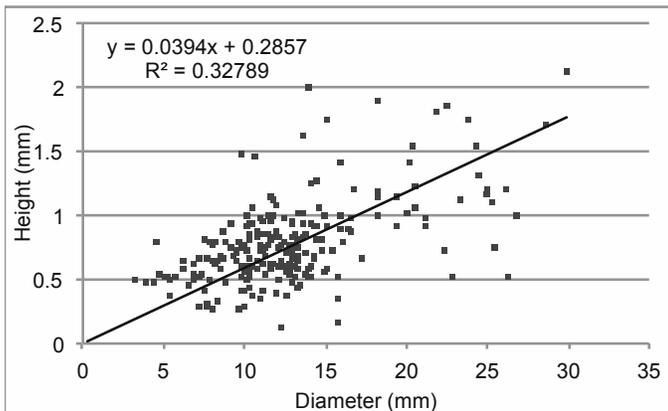


Figure 5. A graph of heights vs. diameters of the *Tribrachidium* Nilpena. Although there is little difference in height across the genus, larger specimens do tend to have slightly more vertical relief.



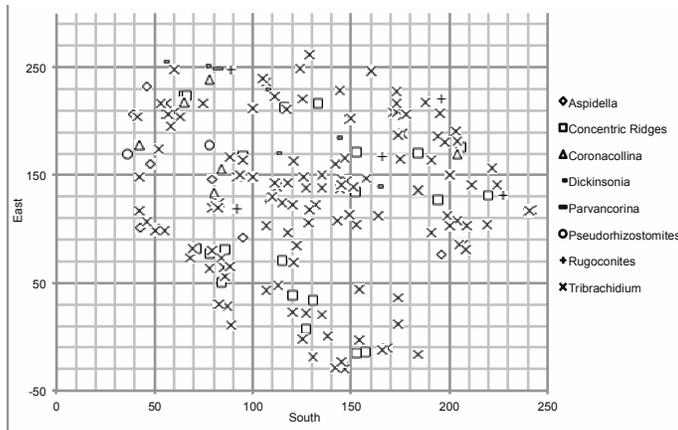
Distribution of *Tribrachidium*

At Nilpena, *Tribrachidium* occurs in four facies; most commonly in the wave-base sand facies, relatively commonly in the sheet-flow sand facies and only rarely in the delta-

front and shoreface sand facies (Gehling and Droser, 2013). In the wave-base facies, *Tribrachidium* occurs on six of twenty-two beds on the base of thin-bedded, rippled quartz sandstones. The rich fossil assemblages of this facies represent benthic communities typically smothered by sand deposited by waning storm-surges.

Tribrachidium dominates one of these beds (1TT), occurring in concentrations of tens per m² (Fig. 6). Additionally, 19 specimens of *Tribrachidium* occur on a second bed (MM3) in this facies with over 400 fossils representing other genera. *Tribrachidium* occurs as a single specimen or a few specimens on four additional beds within this facies.

Figure 6. A plot of the fossils on 1TT. *Tribrachidium* are represented by the X's; concentric ridges are represented by the squares.



The sheet sand facies consists of laterally continuous event beds with tool marks and planar lamination. Ripples are not present, yet beds contain *Tribrachidium* and several other fossils that are most similar to those common in the classic Ediacara Member

rippled facies. *Tribrachidium* dominates one bed (TBEW) of the four representing this facies and occurs on two of the others.

The size and shape of the excavated beds is a function of outcrop and weathering; beds vary from 5-25 m². While edge effects and low sample size are a problem for most of the beds with *Tribrachidium*, a nearest neighbor analysis run using PAST (Hammer et al., 2001) shows that on 1TT *Tribrachidium* are randomly distributed spatially ($R=.911$, $p=.0696$). Anecdotally, there are some examples of *Tribrachidium* fossils touching or nearly touching one another (Fig. 1D), including two on a bed (STCX) that only has three *Tribrachidium* in total. *Tribrachidium* that are touching are also similar in size to one another, with no more than a 5 mm difference in diameter.

Relationship to Textured Organic Surfaces

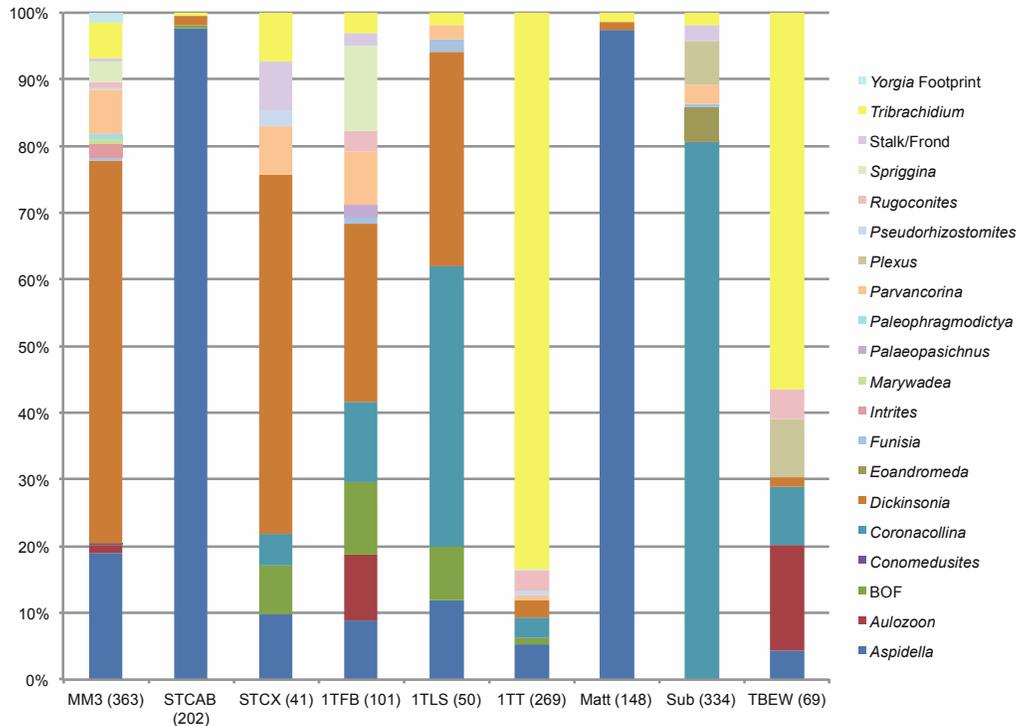
Tribrachidium occurs on beds with varying abundances and types of textured organic surfaces (TOS), which are discrete textural modifications of bedding surfaces, reflecting microbial mats as well as more complicated surfaces with larger-scale patterning, yet not clearly a discrete body fossil (Gehling and Droser, 2009). Of the beds with large numbers of *Tribrachidium*, the lack of extensive bedding plane textures attributed to mats suggest that MM3 had only a thin mat cover (Tarhan et al., 2010), while 1TT is covered with evidence of an extensive textured organic surface with millimeter-scale relief. TBEW shows no evidence of widespread textured organic surfaces, but several of the *Tribrachidium* are associated with discrete patches of the TOS ‘micropucker’ (Gehling

and Droser, 2009). In these examples, a patch of micropucker is located around what would have been the base of the *Tribrachidium* (Fig. 1E), but there is no evidence that the micropucker would have covered any part of the organism. There are also other *Tribrachidium* on the bed not associated with micropucker, as well as other examples of micropucker on the bed not associated with *Tribrachidium*. On each bed, the outer edges of the *Tribrachidium* fossils are clearly defined; none of the surrounding TOS cuts across the edges of the fossils. Because there is also no evidence of TOS overprinting *Tribrachidium*, the live organism was apparently sitting or encrusting upon the mat surface.

Relationship to Other Taxa

Tribrachidium occurs on beds with a wide variety of other taxa, but is not associated statistically with any one other taxon or specific assemblages of taxa (Fig. 7). On TBEW it occurs with *Aulozoon* and *Coronacollina*, both common components in this facies. There are no *Aulozoon* on 1TT, and only a few *Coronacollina*. Although *Tribrachidium* makes up about 80% of the fossils on it, there are also a few *Dickinsonia*, *Aspidella*, and *Spriggina*, which are less common or even absent on TBEW. MM3 is dominated by *Dickinsonia*, and also has several *Aspidella*, as well as larger numbers of *Spriggina* and *Parvancorina*. While there is some overlap in the taxa present on each of these beds, the abundances of the taxa on each bed make them notably different in overall composition.

Figure 7. A stacked bar histogram showing the relative abundance of different fossil taxa and morphologies on beds. Each bar represents a single bed, and the total number of fossils on the bed is listed in parentheses next to the bed name on the x axis. Different colors and patterns represent different taxa or morphologies. *Tribrachidium* is not found consistently in association with a specific taxon or group of taxa. Modified from Droser and Gehling (in press).



Size Frequency Distributions of *Tribrachidium*

Measured *Tribrachidium* range in diameter from 3-38 mm, extending the range in original description of the genus, which reported sizes of up to 26 mm (Glaessner and Daily, 1959). The size frequency distributions of specimens on beds 1TT, MM3, and TBEW, and the distribution for all of the *Tribrachidium* at Nilpena as well as those at the South Australia Museum, are shown in Fig. 8. There is 36 mm of size variability across the 286 *Tribrachidium* examined; however, despite the fact that about 3/5 of these *Tribrachidium* are on 1TT, there is range of only 11 mm for this bed. The range of sizes

of *Tribrachidium* on bed MM3 is also about 11 mm. There is a 22 mm range on TBEW. A Kolmogorov-Smirnov test statistic was run using PAST (Hammer et al., 2001) to compare the size distribution of *Tribrachidium* on each of these beds to the overall size distribution at Nilpena. Additionally, the distributions of MM3 and TBEW are nearly non-overlapping. A Bayesian Information Criterion (BIC) cluster analysis using the mclust package in R also found that three distinct size modes were present in the composite data set consisting of these three beds. Furthermore, the three individual bed populations are best described as single groups (Fig. 9; Fraley and Raftery, 2007). This further confirms the results detected by the Kolmogorov-Smirnov analyses.

Figure 8. The size frequency distribution of all *Tribrachidium* at Nilpena and of selected beds. When fossils were not completely circular, diameter, on the x axis, was measured as widest distance across the specimen. The three beds with the most *Tribrachidium* show that individuals on the same bed tend to be similar in size. Beds MM3 and TBEW almost have non-overlapping distributions.

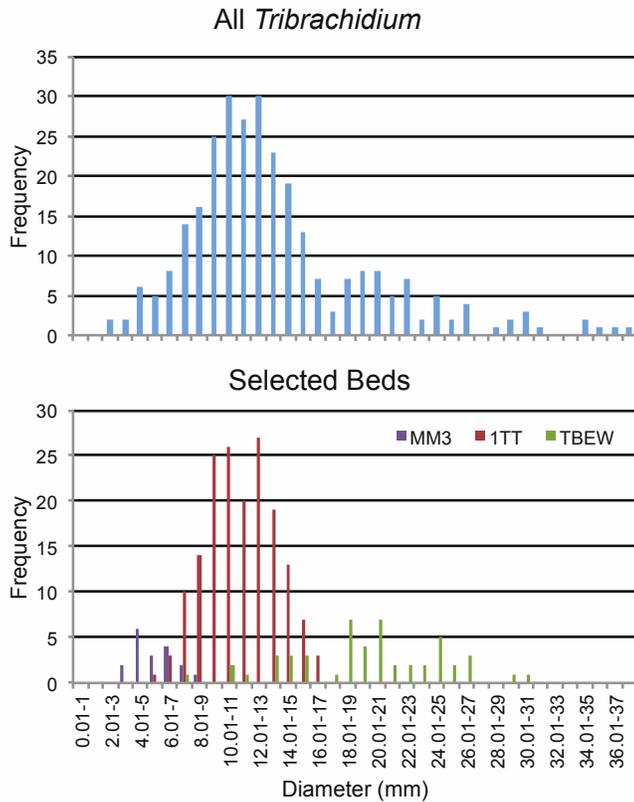
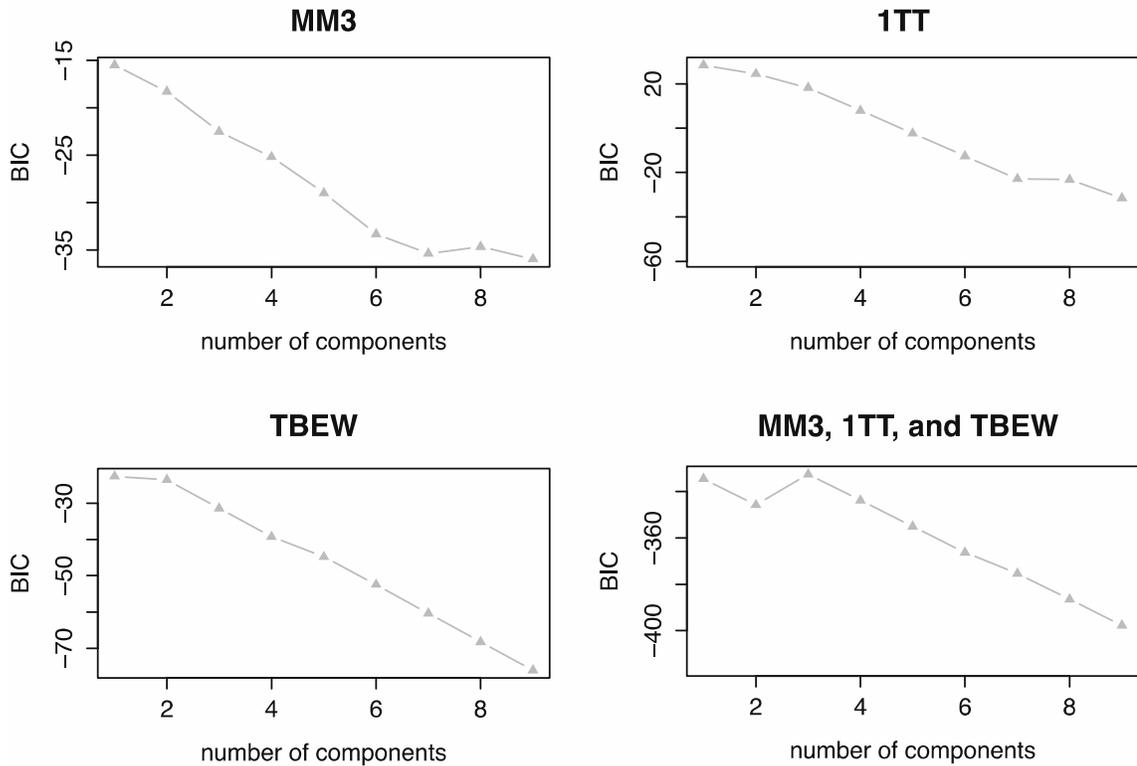


Figure 9. BIC cluster analysis plots for each bed with large numbers of *Tribrachidium*, and for those three beds combined. For each individual bed, BIC resolves single-group solutions, while resolving a three-group solution for the combined beds.



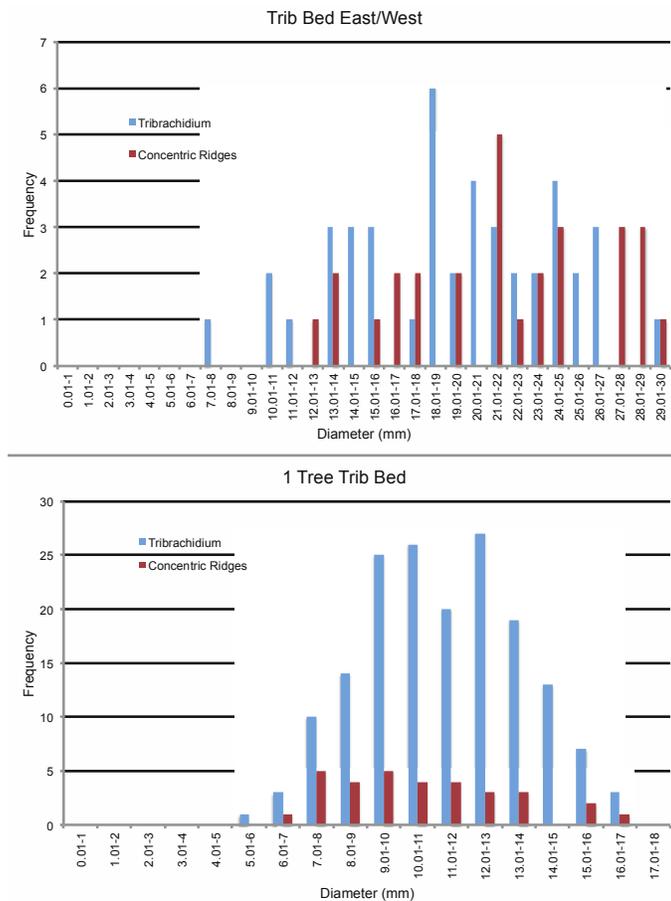
Concentric Ridge Morphology

A discoidal form, consisting of concentric, circular ridges occurs uniquely on beds that are dominated by *Tribrachidium* (Fig. 1F). On 1TT, these fossils are most commonly preserved on the base of the bed as negative external molds in the same manner as *Tribrachidium*, but a few are preserved as positive features on the base of the bed. This morphology also occurs on TBEW, but exclusively in positive relief. When occurring as positive relief, the morphology has superficial similarity to the form genus, *Aspidella*. The number of ridges varies from 2-5. On 1TT, these concentric forms typically have only two or three ridges. Up to five ridges can be found on the well-preserved fossils on

TBEW, but since the preservation of concentric ridges on this bed is typically poor, most only have two clearly visible ridges. Generally, the distance from the center to the first ridge is the smallest, while the distance between ridges tends to be larger at the outer ridges. The relief of the negative external molds varies. The different fossils show a spectrum of specimens where in some show no difference in relief and the ridges appear “nestled” within one another (Fig. 1G), while in others the center rings are slightly higher in relief than the outer rings (Fig. 1H). Some of the concentric ridge fossils on TBEW also have short, fine lines along the outer edge of the fossil, similar to the fringe present on some *Tribrachidium*.

The range of the diameters of 32 concentric fossils on 1TT and 28 from TBEW fall within those of the *Tribrachidium* of their respective beds (Fig. 10). Additionally, a Kolmogorov-Smirnov test statistic was performed using PAST (Hammer et al., 2001) and showed that the size frequency distributions of the concentric ridge form are statistically not significantly different from the distributions of the classic *Tribrachidium* fossils on the same bed (1TT: $D=.208$, $p=.171$; TBEW: $D=.270$, $p=.119$).

Figure 10. Size frequency distributions for the *Tribrachidium* and concentric ridge morphology fossils on TBEW and 1TT. *Tribrachidium* diameters are shown in blue, and concentric ridge diameters are shown in red. The size distribution of concentric ridges on a given bed falls within that of *Tribrachidium* on the same bed.



DISCUSSION

Tribrachidium Distributions

The presence of large *Tribrachidium* on TBEW and small *Tribrachidium* on MM3, both beds with less extensive TOS cover, shows that a presence or a lack of thick organic surface coverage does not have an effect on *Tribrachidium* growth. Other beds with

fewer than five *Tribrachidium* also have varying levels and complexity of TOS coverage. Notably, STCX and STCAB beds both have fairly extensive TOS coverage as well *Tribrachidium* of a similar size to those on TBEW. This indicates that the thick mat coverage on 1TT did not prevent the continued growth of the *Tribrachidium* on that bed. Because *Tribrachidium* is not consistently associated with a particular composition of TOS cover, its distribution was not dependent upon a specific kind of organic surface, nor was thick mat cover prohibitive to its growth and survival.

Importantly, in addition to being found in four of the five facies known from the Ediacaran of South Australia, *Tribrachidium* is the only Ediacara taxon, other than the form genus *Aspidella*, described from South Australia that dominates excavated beds in more than one facies. Because it was able to live in such a diverse array of environments and with a variety of other taxa, *Tribrachidium* can be regarded as an environmental generalist, able to adapt to different physical energies and substrate types. Spatial analyses indicate that *Tribrachidium* on one bed (1TT) was random; however, sample size and bed shape limited this analysis to a single bed. Qualitatively, clusters of *Tribrachidium* are observed on four of the nine beds bearing *Tribrachidium*. In fact, four of the nineteen *Tribrachidium* on MM3, one of the largest beds excavated, fall within the same 10 cm square. The distribution of *Tribrachidium* on the seafloor overall is best described as global and patchy. Furthermore, although the distributions are patchy, they are not associated with any one particular environment.

***Tribrachidium* Populations at Nilpena**

The limited size range of *Tribrachidium* on individual beds relative to its overall size range, and the fact that each of the bed distributions with large numbers of *Tribrachidium* is statistically distinguishable from the overall distribution suggests that *Tribrachidium* populations were composed of cohorts, or groups of similarly-aged individuals. The large size range and resultant smearing effect seen in the bed with the largest *Tribrachidium*, TBEW, is consistent with the expected ontogenetic pattern that there is more variation in the sizes of populations of older organisms than in younger, smaller groups (Grant et al., 1987).

The size frequency distributions of *Tribrachidium* are different from other Ediacara genera, which tend to show consistent distributions across beds. For example, *Aspidella*, a disc-shaped frondose holdfast, has distinctly right-skewed size distributions both on individual beds and when the specimens from localities are considered together (Gehling et al., 2000; Droser et al., 2006). In invertebrates, right-skewed populations typically indicate high infant mortality (Brenchley and Harper, 1998). The *Tribrachidium* populations studied here are not strongly left- or right-skewed. While normal distributions in fossil assemblages are typically interpreted as a result of mechanical sorting (Hammer and Harper, 2005), these beds preserve temporally instantaneous “snapshots” of the seafloor with minimal transport (Gehling, 1999; Droser et al., 2006), further supporting the view that *Tribrachidium* populations comprise single generations. Darroch et al. (2013) studied three rangeomorph and one non-rangeomorph taxa, finding

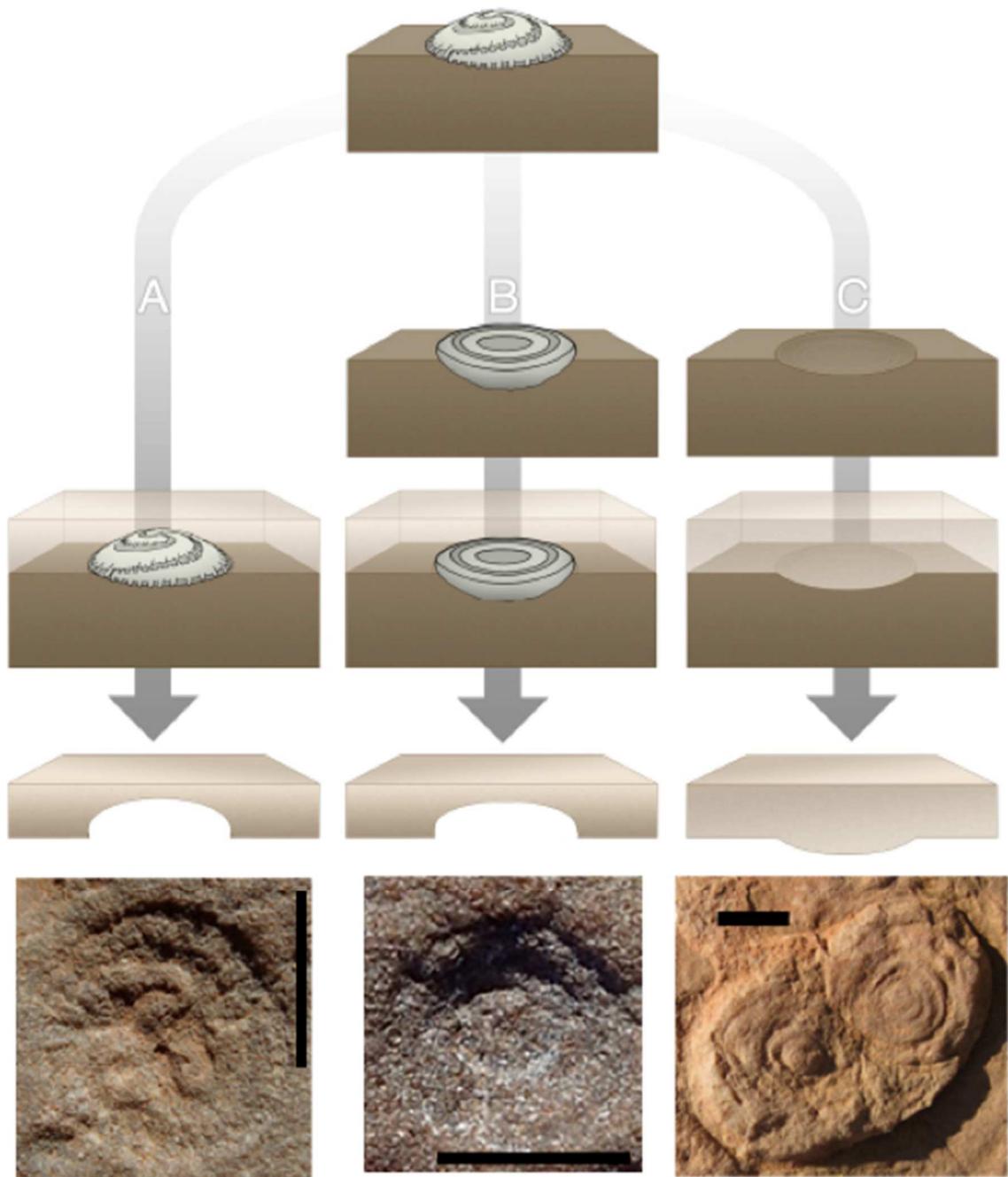
that they also showed consistent right-skewed size distributions across different fossil surfaces. In contrast with *Tribrachidium*, the minimum sizes of each genus were equivalent across the different surfaces; hence, the resultant large size range on each surface led them to favor a continuous reproduction model.

The distinct size groupings of *Tribrachidium* on individual beds provide insight into the reproductive habits of these organisms. Droser and Gehling (2008) found evidence for sexual reproduction in the Ediacara biota in the presence of synchronous aggregate growth in *F. dorothea*. Cohorts, such as those recorded in *Tribrachidium*, can be indicative of either a seasonal or opportunistic sexual reproductive strategy in modern marine invertebrates. In a seasonal reproduction model, recruitment occurs in seasonal cycles and is commonly triggered by factors such as changes in photoperiod (Young, 2003), and has been observed in several marine invertebrate taxa, including both poriferans and cnidarians (Young, 2003; Conn, 2000). Hellstrom et al. (2010) also describe a coral species that reproduces once annually on a species scale but also on a population scale during different but distinct full moons. Distinct cohorts can also result from an opportunistic reproductive strategy, whereby environmental factors that are not directly related to seasons dictate the patterns of reproduction in a species (Tyler and Young, 1992). Some marine invertebrates, often benthic, deep-sea species, seem to combine seasonal and opportunistic reproductive strategies, notably holothurians and sea anemones (e.g. Billett and Hansen, 1982; Tyler et al. 1982; Wigham et al., 2003; Mercier and Hammel, 2009).

Concentric Ridges

The concentric ridge fossils are indistinguishable in size frequency distributions and have a bed distribution identical to *Tribrachidium*, suggesting that concentric ridge fossils are linked to *Tribrachidium*. Specifically, the preservation of these forms suggests that the concentric ridge form is the fossil of the base of the three-armed *Tribrachidium*. This is consistent with previous descriptions of *Tribrachidium* describe the base of the organism as having concentric grooves (Glaessner and Wade, 1966; Fedonkin, 1985). Surprisingly, and unlike other Ediacara organisms, the base of *Tribrachidium* is preserved in two modes – as a positive cast and as a negative mold, both on the base of the bed (Fig. 11). We interpret that the negative external mold is formed when the organism is flipped upside-down prior to or during burial; deposited sand covers an upside-down organism or the base of the *Tribrachidium*. Conversely, a positive cast is formed when the organism is moved out of place prior to burial, and the incoming sand fills the hollow in the mat left by the organism. Because the impression is preserved, rather than the actual base of the organism, the ridges of these fossils are often less distinct than those of the negative external molds on 1TT. The presence of both positive and negative concentric ridge fossils make flipping, and its different preservation possibilities, a tenable hypothesis compared to others that could result in different forms falling within the same distributions, such as sexual dimorphism. Sexual dimorphism is unlikely because the ratios of *Tribrachidium* to concentric ridge fossils on 1TT and TBEW are profoundly different, and because concentric ridge fossils are not present on any other beds.

Figure 11. A diagram of the various modes of preservation observed for *Tribrachidium* at Nilpena. The top image shows a reconstruction of *Tribrachidium* as it would have looked sitting on the seafloor. Column A shows how the typical, three-armed *Tribrachidium* fossils are preserved. When sand buries the organism, a negative external mold of the top of the organism is formed in the base of the sand bed that buries it, resulting in the negative impression that we find. Column B shows how negative external concentric ridge molds are formed. Here, the organism must have been flipped upside down prior to or during burial. It is buried in that orientation, resulting in a negative external mold of the base of the organism on the base of the bed that buried it. Column C shows how positive impressions of concentric ridges are formed on the base of a bed. Here, the organism was moved out of place before or during burial, but the base of the organism left an impression in the mat it was sitting on. That impression is filled with incoming sand during the storm event, creating a positive concentric ridge impression on the base of the bed formed by the incoming sand. The photographs below show the corresponding fossil form that results from each scenario. Scale bars in the photographs are each 1 cm.



There are several explanations for distribution of positive casts or negative molds on 1TT and TBEW. On 1TT, the *Tribrachidium* are small, the mat is thick, and the concentric ridges are almost entirely negative external molds. On TBEW, the *Tribrachidium* are

large, the mat is thin, and the concentric ridges are preserved as positive features. One possibility is that *Tribrachidium* on TBEW were bigger and had therefore been resting overlong on the seafloor; hence, hollows were more likely to form than in the case of the smaller *Tribrachidium* on 1TT. Alternatively, if a small hollow is formed by removal of a *Tribrachidium* on 1TT, the thick mat could have covered or obscured it, especially if it was upside down before the deposition of the overlying sand.

The flipping of *Tribrachidium* provides further insight into their ecology. First, flipping seems to be unique to *Tribrachidium*; there are no other known examples, nor evidence of flipping on the excavated Nilpena beds. Second, we find evidence of *Tribrachidium* flipping on two very different beds. While this process might be expected on a higher energy event bed such as TBEW, the concentric ridge morphology is more common on the low-energy 1TT. While it seems unlikely that *Tribrachidium* could be flipped in a low-energy environment, such conditions may also have played a role in the preservation of upside-down *Tribrachidium* on the bed. A high-energy environment would have washed organisms away completely after flipping. The lack of other marks such as “mop”, structures of stalks and holdfasts pulled by a current (Tarhan et al, 2010), on the bed near the concentric ridge fossils, particularly the positive impressions, may indicate that *Tribrachidium* was not firmly attached to the substrate. This could explain the presence of concentric ridge fossils on a low energy bed, such as 1TT. The relief of positive features shows that sediment built up around the base of the organism over time, and that *Tribrachidium* was stationary, until moved by environmental forces.

An alternative hypothesis explaining the negative external mold concentric ridges on 1TT involves biostratinomic processes. Some of the organisms on the bed likely died prior to the event that buried the bed. It is possible that the three-armed surface decayed away, leaving the internal structure exposed at the time of burial. If the internal structure of the organism mirrors the concentric ridge base, these decayed organisms would be preserved as negative external concentric ridge molds on the base of the resulting bed.

Superficially, the positive concentric ridge features on TBEW resemble *Aspidella*, but their distribution is, unlike published reports of *Aspidella* (Gehling et al., 2000; Droser et al., 2006; Tarhan et al., 2010; Tarhan et al., 2015), not right-skewed. Additionally, fine, faint ridges are preserved on the outer edges of some of these concentric ridge fossils, a feature not reported in *Aspidella*. Considering these factors, the most parsimonious conclusion is that these concentric ridge fossils are preservations of the base of *Tribrachidium* that result from the removal of the organism.

CONCLUSIONS

Tribrachidium is a globally-distributed member of the Ediacara biota. In South Australia, the distribution of *Tribrachidium* on the Ediacaran seafloor overall is best described as patchy, dominating a few beds and common in small numbers on other beds.

Tribrachidium-bearing beds vary greatly in many respects; they come from different facies, have different assemblages of taxa, and are covered with textured organic surfaces of different varieties and to different extent. *Tribrachidium* may have been an environmental generalist, able to adapt to different environments, and indeed dominate

communities and thus, thrive in environments that differed greatly in aspects such as fluid flow and depth.

The size frequency distributions of *Tribrachidium* suggest that these organisms lived in cohort populations. The overall size range of this taxon is larger than recorded on individual beds, and their distributions are statistically distinguishable from the overall range of the genus. *Tribrachidium* likely reproduced on a seasonal cycle, or possibly opportunistically, but was not a continuous reproducer.

The most parsimonious explanation for the concentric ridge forms found on beds dominated by *Tribrachidium* is that they are alternative preservations of *Tribrachidium*. They were fossilized after the organism was removed from its place on the seafloor or flipped upside-down or decayed. The size distributions of these concentric ridges match those of the *Tribrachidium* on the same bed. The methods of preservation, specifically the presence of positive and negative features, support this hypothesis. This process has not been described in other members of the Ediacara biota, providing a unique look into the biostratigraphy of these organisms.

The inclusion of concentric ridge fossils in the counts of *Tribrachidium* does not change the result that the distributions of *Tribrachidium* on those beds are statistically distinguishable from one another, nor does it change the size range for the *Tribrachidium* on the same bed. Caution should be used when including positive concentric ridges (such as those on TBEW) in counts of the total *Tribrachidium* on a bed, since the nature of their

preservation does not preclude the possibility of that organism's presence elsewhere on the bed.

Studying the ecology of *Tribrachidium* has allowed us to constrain several aspects of its biology and ecology. *Tribrachidium* lived in patches of generally similar-sized individuals across the seafloor. These patches were not restricted to specific environments, energy levels, organic mat cover, or the presence of specific other taxa, and the size distributions of individual populations suggest that *Tribrachidium* reproduced seasonally or opportunistically. The data and observations described here provide new insight into the lifestyle of *Tribrachidium* and demonstrate that it was distinctive from other Ediacara taxa.

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APPENDIX A

Location	Specimen	Avg Diam (mm)	Height (mm)	Arm (mm)	Edge (mm)
MM3	437s/441e	4.67	0.55		
MM3	490s/361e	5.73	0.53		
MM3	515s/194e	8.05	0.65		
MM3	434s/301e	4.6	0.8		
MM3	258s/260e	4.95	0.51		
MM3	270s/264e	3.28	0.49		
MM3	662s/330e	7.89	0.49		
MM3	662s/236e	13.92	0.51	3.9	0.7
MM3	37s/310e	3.95	0.47		
MM3	728s/337e	5.41	0.5	2.7	0.7
MM3	365s/437e	6.78	0.62	1.7	0.6
MM3	39s/278e	6.14	0.59		
MM3	161s/254e	4.45	0.47	1.2	0
MM3	259s/259e	5.27	0.53	1.1	0
MM3	649s/319e	7.13	0.67	1.5	0.2
MM3	432s/434e	6.387			
MM3	435s/438e	4.12			
MM3	435s/427e	6.955			
MM3	426s/216e	4.129			
1TT	60s/209e	14.02	0.52		
1TT	75s/216e	13.43	0.45		
1TT	63s/204e	9.25			
1TT	100s/212e	10.3	0.82	2	0.6
1TT	170s/103e	11.9	0.87		
1TT	121s/163e	12.12	0.49	3.5	1.5
1TT	58s/195e	15.95	1.01	4.1	1.6
1TT	41s/204e	7.25	0.3	2.5	0.6
1TT	184s/171e	8.22	0.63	1.5	0.6
1TT	111s/223e	13.24	0.82	3.5	0.9
1TT	149s/202e	15.44	0.72	3.8	1
1TT	150s/203e	10.4	0.38	1.7	1.7
1TT	52s/174e	9.14			
1TT	85s/64e	13.26	0.64	2.8	1.8
1TT	88s/65e	13.01	0.66	2.8	1.4
1TT	78s/63e	12.97	0.71	2.9	1.8

1TT	60s/248e	8.2	0.79		
1TT	129s/262e	7.25	0.51		
1TT	173s/217e	13.05	0.85	3.1	1.7
1TT	140s/202e	11.69	0.61		
1TT	176s/188e	13.2	1.03	2.7	1.5
1TT	125s/221e	8.86	0.8	1.6	0.1
1TT	144s/229e	13.75	0.54	3.3	2.2
1TT	107s/237e	10.08	0.49	1.5	0.5
1TT	105s/240e	10.9	0.72	2.3	0.7
1TT	160s/247e	15.82	0.16	2.9	1.1
1TT	126s/248e	11.86	0.62		
1TT	142s/160e	13.24	0.75	2.9	1.4
1TT	188s/218e	12.05	0.6	2.6	1.8
1TT	126s/248e	9.14		2.4	1.7
1TT	124s/249e	10.18	0.99	2.4	0.6
1TT	135s/138e	11.19	0.95		
1TT	132s/123e	11.25	0.55	2.5	1.4
1TT	143s/108e	8.46	0.69		
1TT	173s/228e	16.41	0.9	4.1	2.4
1TT	200s/103e	8.88		2.4	1.5
1TT	176s/205e	12.23	0.62	2.2	1.5
1TT	176s/207e	13.61	1.02	1.7	2.5
1TT	171s/208.5 e	13.03	0.61	3.1	1.2
1TT	183s/209e	13.36			
1TT	199s/112e	16.5	0.88	3.4	1.8
1TT	191s/164e	8.48	0.58		
1TT	200s/150e	14.18	0.66	4.1	1.4
1TT	203s/191e	9.92	0.29	1.7	0.6
1TT	198s/181e	10.31	0.86	2.4	1.2
1TT	224s/141e	8.59	0.66		
1TT	194s/186e	13.94	0.59	2.8	1.5
1TT	200s/103e	12.04	0.84		
1TT	222s/157e	11.39	0.86	2	1.1
1TT	207s/85e	7.25			
1TT	205s/85e	10.99	0.98		
1TT	208s/81e	8.89	0.47	1.7	1
1TT	204s/108e	13.67	0.93	3.6	1.8
1TT	242s/118e	9.75	0.6		

1TT	219s/105e	6.52	0.45		
1TT	240s/116e	14.41	0.91	4.2	1.9
1TT	241s/117e	8.01	0.77	1.5	0.6
1TT	55s/99e	12.86	0.95	2.8	1.5
1TT	50s/99e	15.78	0.51	4	1.6
1TT	184s/136e	8.37	0.34		
1TT	86s/56e	13.29	0.59	3	1.1
1TT	122s/84e	12.73	0.58	2	1.2
1TT	164s/112e	9.285	0.68	1.1	0.8
1TT	42s/117e	9.21	0.76	1.2	1.1
1TT	195s/208e	7.45	0.82		
1TT	128s/106e	13.23	0.68	2.9	1.5
1TT	46s/107e	14.33	0.68	3.7	1.2
1TT	118s/97e	9.95	0.57		
1TT	83s/125e	7.6	0.32	2.2	1.4
1TT	82s/120e	10.37	0.44	2.5	1.6
1TT	81s/121e	13.26	0.44	2.9	1.6
1TT	79s/120e	12.95	0.48	3.2	1.8
1TT	211s/142e	10.32	0.56		
1TT	127s/138e	11.77	0.83	2.8	1.2
1TT	42s/148e	16.1	0.79	3.3	2
1TT	135s/150e	14.17	0.61	2.8	2.1
1TT	144s/137e	12.88	0.72	3	1.4
1TT	151s/139e	9.13	0.93	2.1	1
1TT	148s/145e	8.9		3	0.9
1TT	145s/141e	9.42	0.64	2	0.5
1TT	145s/147e	9.47	0.71		
1TT	92s/148e	15.74	0.36	2.7	3.2
1TT	93s/150e	9.78	0.42		
1TT	129s/118e	10.88	0.86		
1TT	88s/167e	10.22	0.94		
1TT	191s/97e	10.29	0.6		
1TT	132s/123e	11.27	0.75	2.2	1.6
1TT	84s/73e	11.2	0.41	2	0.7
1TT	149s/114e	10.4	0.94	1.9	1
1TT	153s/105e	11.97	0.39	2.1	1.1
1TT	68s/73e	10.93	0.78	2.1	1
1TT	147s/166e	12.04	0.76	2.1	1.3
1TT	100s/148e	14.84	0.99	2.9	2.4

1TT	112s/139e	10.7	1.45	2.3	0.8
1TT	118s/143e	12.67	0.56	2.1	0.9
1TT	111s/143e	9.98	0.57	2	0.8
1TT	211s/142e	9.99	0.78	2.4	1
1TT	170s/161e	5.3	0.38		
1TT	52s/174e	9.77	0.51		
1TT	56s/217e	11.62	0.63		
1TT	88s/167e	9.77	1.48		
1TT	174s/187e	9.3			
1TT	117s/211e	9.82	0.76	2.1	0.9
1TT	175s/165e	10.77	0.83		
1TT	204s/182e	12.96	0.77	2.8	1.8
1TT	195s/147e	7.34	0.55	1.3	0.5
1TT	109s/129e	12.72	0.55	2.8	1.5
1TT	110s/130e	11.07	0.62	2.3	0.6
1TT	43s/202e	7.51	0.42		
1TT	41s/204eB	11.36	0.69		
1TT	121s/69e	10.78	0.65	2.4	0.9
1TT	121s/70e	10.47	0.6	2.7	1.1
1TT	79s/80e	14.89	0.57		
1TT	69s/82e	10.3	0.67		
1TT	FL-1a	9.99			
1TT	FL-1b	10.85			
1TT	FL-2	9.9	0.42		
1TT2	125s/-2e	10.8	0.59	3.5	1.4
1TT2	147s/-30e	12.6	0.7	2.6	1
1TT2	142s/-29e	14.1	0.93	2.3	1.3
1TT2	135s/21e	11.8	1.13	2.7	1.1
1TT2	127s/22e	11.5	1	1.7	2.3
1TT2	168s/-11e	12.8	0.77	2.9	1.4
1TT2	166s/-12e	12.4	0.61	2.9	1.5
1TT2	154s/44e	10.9	0.35	3.2	0.9
1TT2	145s/-23e	12.6	0.37	2.8	1.6
1TT2	184s/-16e	9.7	0.26	1.5	1
1TT2	107s/43e	7.7	0.67		
1TT2	89s/11e	12.4	0.98	3.2	1.2
1TT2	131s/-19e	9.4	0.72		
1TT2	113s/48e	8.6	0.67	1.5	0.6
1TT2	87s/28e	12.2	0.77	3	1.5

1TT2	82s/31e	6.9	0.5	0.7	0.5
1TT2	174s/36e	9.8	0.77		
1TT2	138s/1e	14	2.01	3.3	1.5
1TT2	154s/-3e	11.2	0.72	2.4	1.1
1TT2	120s/23e	7.6	0.3		
1TT2	93s/31e	8.4	0.64	1.7	0.8
1TT2	174s/12e	10.1	0.92	1.8	1.2
1TTA	1	8	0.27	1.2	0.5
1TTA	2	9.7	0.8		
1TTA	3	10.5	1.06	1.5	1
1TTA	4	12.9	0.94	2.2	1.4
1TTA	5	14.5	0.81	2.7	1.6
1TTA	6	10.2	0.49	2.1	1
1TTA	7	9.1	0.75		
1TTA	8	15	0.58	2.5	1.5
1TTA	9	12.4	0.8	2.8	1.5
1TTA	10	11.6	0.82	2.5	2
1TTA	11	11.9	1.08	2.3	2.5
1TTA	12	12.8	0.75	2.3	1.5
1TTA	13	8.7	0.87	1.5	1
1TTA	14	11.7	0.59	2.1	1.2
1TTA	15	14.6	1.06	2.4	1.5
1TTA	16	11.8	0.99	1.9	0.7
1TTA	17	6.8	0.55		
1TTA	18	15.1	0.92	3.6	1.9
1TTA	19	13	0.84	2.9	1.4
1TTA	20	12.7	0.59	2.2	1.2
1TTA	21	12.2	0.64	2.2	1.3
1TTA	22	12.7	0.62	2.3	1.2
1TTA	23	14.8	0.81	2.1	2.2
1TTA	24	10.1	0.72	2	1.7
1TTA	25	14.4	1.27	2.4	2.5
1TTA	26	13.7	0.7	1.3	1.8
1TTA	27	13.6	0.83	3.3	2.1
1TTA	28	12.2	0.12	2	1.7
1TTA	29	10.2	0.6	1.6	2
1TTA	30	15.9	0.99	2.5	3.1
1TLS	156s/136e	16.64	0.97		
1TFB	162s/83e	12.03	0.85	3.7	0.8

1TFA	707s/640e	11.63	0.96		
1TFA	654s/733.5e	6.11	0.64		
1TFA	762s/669e	11.46	0.77		
1T float	1TFL1	7.28			
AB	239s/271e	28.665	1.71	7.85	3.05
X	419s/559e	16.72	1.2		
X	411s/522e	21.25	0.92	6.2	2.4
X	414s/522e	22.275	0.73		
TBEW	183s/490e	26.76	1.01	7	3
TBEW	223s/490e	24.24	1.55	4.8	3.5
TBEW	188s/485e	20.6	1.07	5.3	2
TBEW	198s/437e	15.83	0.9	3.9	2.1
TBEW	190s/480e	20.28	1.54	4.2	2.7
TBEW	173s/452e	18.21	1.18	5.2	2.4
TBEW	197s/343e	25.39	0.74	6.3	3
TBEW	158s/370e	24.99	1.16	4.9	3
TBEW	193s/364e	22.84	0.53	4.6	3.3
TBEW	223s/372e	18.23	1.14	3.6	2.6
TBEW	126s/287e	19.36	0.92	5.4	1.5
TBEW	135s/113e	11.59	1.15	2.4	1.3
TBEW	87s/67e	13.8	0.86	3.35	1.7
TBEW	103s/113e	14.13	1.26	2.65	1.8
TBEW	169s/208e	26.04	1.21	6.5	3.55
TBEW	58s/46e	7.8	0.79		
TBEW	122s/134e	26.21	0.52	5.7	3
TBEW	108s/147e	20.455	1.22	5	3.2
TBEW	108s/149e	24.555	1.31	6.4	3.5
TBEW	246s/298e	14.27	0.91	3.45	1.65
TBEW	150s/138e	14.725	0.73	3.5	1.6
TBFL	TBFL1	23.85	1.75	5.7	3.3
TBFL	TBFL2	22.43	1.85	7.3	3.2
TBFL	TBFL3	20.05	1.03	6.1	2.4
TBFL	TBFL4	23.32	1.12		
TBFL	TBFL5	17.25	0.67	4.4	2.3
TBFL	TBFL6	10.86	0.88	2	0.6
TBFL	TBFL7	10.33	0.52	2.3	0.9
TBFL	TBFL9	15.98	1.42	3.9	1.6
TBFL	TBFL10	13.66	1.63		

TBFL	TBFL11	18.28	1	5.4	1.8
TBFL	TBFL13	22.21			
TBFL	TBFL14	29.9	2.12	6.3	3
TBFL	TBFL15	15.03	1.75	3.6	2
TBFL	TBFL16a	18.205	1.89	4.5	2.5
TBFL	TBFL16b	20.16	1.41	6.5	3.3
TBFL	TBFL17	25.26	1.11	5.7	4.1
TBFL	TBFL18	24.93	1.21	5.5	2.8
TBFL	TBFL19	21.85	1.81	5.5	2.3
TBFL	TBFL20	19.33	1.14		
TBFL	TBFL21a	18.45			
TBFL	TBFL21b	18.4			
TBFL	TBFL22	13.04	0.53	2.3	1.1
TBFL	TBFL23	21.16	0.97	4.9	1.9
TBFL	FL1Ta	19			
TBFL	FL1Tb	21			
TBFL	FL1Tc	20			
TBFL	FL2Ta	31			
TBFL	FL2Tb	25			
TBFL	FL4Ta	20			
Container	N12-23	11.12	3.1	0.8	
SAM	P14313a	20			
SAM	P14313b	20			
SAM	P14247	16			
SAM	P14314	21			
SAM	P40393	22			
SAM	P14320	15			
SAM	P43268	27			
SAM	P40980	23			
SAM	P14316	23			
SAM	F16723a	13			
SAM	F16723b	11			
SAM	P40957a	31			
SAM	P40957b	21			
SAM	P43259	32			
SAM	P40941	16			
SAM	P40403	17			
SAM	P40396	38			
SAM	P14317a	20			

SAM	P14317b	12			
SAM	P42662	12			
SAM	P42083	6			
SAM	P40937a	35			
SAM	P40937b	20			
SAM	P40937c	14			
SAM	P40405	35			
SAM	P40402a	15			
SAM	P40402b	12			
SAM	P40397	23			
SAM	P40404	16			
SAM	P18620	37			
SAM	P42136	18			
SAM	P40394	30			
SAM	P40401	17			
SAM	P44816a	3			
SAM	P44816b	3			
SAM	P14311	18			
SAM	P40398	15			
SAM	P49337	31			
SAM	P41630	9			
SAM	P49339	36			

Measurements of *Tribrachidium* used in this study. Location indicates where at Nilpena the specimen is found, or if it is located at the South Australia Museum (SAM). Specimen indicates the specimen's coordinates on the bedding plane, its location on a slab, or its museum identification number. Avg Diam is the average diameter (in mm) as measured from each available latex of that specimen. Height is the measurement of relief (in mm) of each specimen. Arm indicates the distance (in mm) from the center to the bed in the arm, and Edge indicates the distance (in mm) from the bend in the arms to the edge (see Figure 4). Height, Arm, and Edge could not be accurately measured in all specimens.

APPENDIX B

Location	Specimen	Avg Diam (mm)
1TT	45s/206e	11.08
1TT	115s/71e	15.78
1TT	116s/213e	9.34
1TT	78s/78e	10.69
1TT	71s/82e	9.78
1TT	65s/224e	11.07
1TT	66s/224e	13.74
1TT	195s/67e	9.6
1TT	133s/217e	8.56
1TT	86s/81e	12.17
1TT	194s/127e	8.41
1TT	220s/132e	11.04
1TT	153s/172e	10.52
1TT	152s/135e	7.85
1TT	196s/77e	7.33
1TT	206s/176e	12.51
1TT	95s/168e	8.92
1TT	184s/171e	6.55
1TT2	146s/-29e	10.9
1TT2	157s/-14e	8.8
1TT2	153s/-15e	16.7
1TT2	84s/51e	11.7
1TT2	131s/34e	10.6
1TT2	120s/39e	7.7
1TT2	127s/7e	7.8
1TTA	CC1	13.9
1TTA	CC2	9.3
1TTA	CC3	9.4
1TTA	CC4	12.5
1TTA	CC5	7.1
1TTA	CC6	13.4
1TTA	CC7	15.4
TBEW	182s/350e	13.8
TBEW	221s/278e	15.9
TBEW	120s/113e	19.8

TBEW	109s/165e	17.2
TBEW	178s/366e	17
TBEW	146s/388e	19.7
TBEW	572s/438e	12.1
TBEW	126s/184e	28.4
TBEW	104s/133e	28.2
TBEW	197s/516e	21.3
TBEW	140s/420e	23.2
TBEW	221s/362e	17.2
TBEW	88s/114e	24.7
TBEW	93s/111e	24.7
TBEW	218s/487e	21.4
TBEW	233s/296e	28
TBEW	234s/297e	23.3
TBEW	150s/209e	29.1
TBEW	67s/39e	28.9
TBEW	FL1	27.4
TBEW	FL2	22.4
TBEW	FL3a	21.3
TBEW	FL3b	16.1
TBEW	FL3c	24.4
TBEW	Slab22	14
TBEW	49n/39w	21.88
TBEW	52n/65w	27.24
TBEW	77n/265w	21.59

Measurements of the concentric ridge fossils used in this study. Table headings are the same as used in Appendix A.