Title: Paleoecology of the enigmatic *Tribrachidium*: new data from the Ediacaran of South Australia

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Abstract

Tribrachidium is a monospecific genus of the Ediacara biota found globally. In the Ediacara Member of the Rawnsley Quartzite, 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 single generations. 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 of 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 dead and partially decayed prior to burial.

Key words: *Tribrachidium*, Ediacara Biota, South Australia, paleoecology, population dynamics

1. 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, as well as in 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, 2015). 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 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 some 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 "bullae" found near the bend in each of the arms has been interpreted, without any other evidence, as a possible gonad or reproductive structure (Jenkins, 1992). Specimens collected in the Chace Range, 50 km southeast of Nilpena are more conical than others from elsewhere, 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 in 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.

2. 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 from the wave-base and sheet-flow sands facies multiple square meters in size have been excavated and analyzed. Biodiversity is highest in the wave-base sand facies. Table 1 details the facies, area, and number of *Tribrachidium* for each *Tribrachidium*-bearing bed excavated at Nilpena. Fossils are typically preserved as molds on the base of beds.

99 **Table 1**

100 Facies designations and areas of *Tribrachidium*-bearing beds at Nilpena

Bed	Facies	Area (m ²)	Number of <i>Tribrachidium</i>
MM3	wave-base	21.25	19
STCAB	wave-base	3.44	1
STCX	wave-base	9.35	3
1TFB	wave-base	8.78	4
1TLS	wave-base	2.07	1
1TT	wave-base	5.02	169
Matt	sheet-flow	3.29	2
Sub	sheet-flow	3.94	6
TBEW	sheet-flow	3.5	43

101

102 These beds preserve temporally instantaneous “snapshots” of the seafloor, generally
 103 with minimal transport (Gehling, 1999; Droser et al., 2006). Criteria for determining
 104 the amount of transport or sorting on these beds include indications of current
 105 alignment, as in from pull out structures (Tarhan et al., 2010) or *Dickinsonia* lift
 106 structures (Evans et al., 2015), the nature and extent of microbial mat coverage
 107 (Gehling and Droser, 2009) and size sorting across taxa. These features suggestive
 108 of transport are easily identified and occur on a few of the excavated beds at
 109 Nilpena, but the *Tribrachidium*-bearing beds have no indication of extensive
 110 transport or sorting.

111

112 To date, 26 fossiliferous beds comprising a total of more than 300 square meters of
 113 Ediacaran-aged seafloor have been excavated at Nilpena. Of these, 22 are from the
 114 wave-base facies and 4 are from the sheet-flow facies. Because the fossils are
 115 preserved on bed bases, these beds are inverted during excavation to expose their
 116 bases before they are reassembled. The beds are then marked into square meter

117 grids, and the locations of fossils are recorded with respect to the grid to create a
118 record of the species, abundance, and spatial distribution of the individuals on the
119 bed.

121 **3. Methods**

122 Latex molds were made of all of the *Tribrachidium* on the beds at Nilpena.
123 Additionally, all known float specimens of *Tribrachidium*, as well as all of those
124 specimens housed at the South Australia Museum, were also photographed and
125 measured. The diameter of each fossil was measured from the latex using digital
126 calipers. Partial specimens were used only when more than half of the organism was
127 preserved. Specimens found on the excavated beds have been left in place to enable
128 further bed-scale research at the site.

130 A nearest-neighbor analysis was used to determine the spatial distribution of
131 *Tribrachidium* across a single bedding plane. The Kolmogorov-Smirnov statistic
132 provides a statistical comparison of the shapes and positions of two univariate
133 distributions, and was used to compare the size frequency distributions of the three
134 beds with the most *Tribrachidium*, as well as the size frequency distributions of
135 *Tribrachidium* and concentric ridges on the same bed. Both the nearest-neighbor
136 statistic and the Kolmogorov-Smirnov analyses were conducted using the PAST
137 software (Hammer et al., 2001). A Bayesian Information Criterion (BIC) cluster
138 analysis was conducted using the mclust package in R (Fraley and Raftery, 2007) to

determine the most likely number of groupings in different populations of *Tribrachidium* based on body size (diameter).

4. 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 grain size 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.

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. 4), 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. The consistently round shape of these soft-bodied organisms may also be further indication that they were buried in place, rather than transported.

5. Distribution of *Tribrachidium*

In South Australia, *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). Specimens from the latter two facies are not known from *in situ* bedding planes, but rather from float now located at the South Australia museum. In the wave-base facies, *Tribrachidium* occurs on six of twenty-two beds on the base of thin-bedded, rippled quartz sandstones. *Tribrachidium* dominates one of these beds (1TT), occurring in concentrations of tens per m² (Fig. 5). 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.

The sheet-flow 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, a result of the irregular shape of most beds, are a problem for most of the beds with *Tribrachidium*, a nearest-neighbor analysis run using PAST (Hammer et al., 2001) shows that on bed 1TT, *Tribrachidium* are randomly distributed spatially ($R=.911$, $p=.0696$). Anecdotally, there are rare examples of *Tribrachidium* fossils touching or nearly touching one another (Fig. 1D), including two on bed STCX, which only has three *Tribrachidium* in

total. The few *Tribrachidium* that are touching are also similar in size to one another, with no more than a 5 mm difference in diameter. Additionally, four of the nineteen *Tribrachidium* on MM3, one of the largest beds excavated, fall within the same 10 cm square.

6. Relationship of *Tribrachidium* to textured organic surfaces and other taxa

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.

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. 6). 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 this bed, 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.

7. Size frequency distributions of *Tribrachidium*

Measured *Tribrachidium* range in diameter from 3-38 mm, extending the size 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. 7. 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 analysis 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. The size frequency distributions of each of the beds were found to be statistically significantly different from both the overall size frequency distribution for *Tribrachidium* in South Australia (field and museum specimens), and from one another. (All vs. MM3: $D=.813, p<.<.001$; All vs. 1TT: $D=.237, p<.<.001$; All vs. TBEW: $D=.523, p<.<.001$; TBEW vs. 1TT: $D=.750, p<.<.001$; TBEW vs. MM3: $D=.927, p<.<.001$; MM3 vs. 1TT: $D=.859, p<.<.001$) 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. 8; Fraley and Raftery, 2007). This further confirms the results detected by the Kolmogorov-Smirnov analyses.

8. 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); in others the near-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. 9). Additionally, a Kolmogorov-Smirnov analysis 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: $D=.270$, $p=.119$).

9. Discussion

9.1. *Tribrachidium* distributions

275 The presence of large *Tribrachidium* on TBEW and small *Tribrachidium* on MM3,
276 both beds with less extensive TOS cover, shows that a presence or a lack of thick
277 organic surface coverage does not have an effect on *Tribrachidium* growth. Other
278 beds with fewer than five *Tribrachidium* also have varying levels and complexity of
279 TOS coverage. Notably, STCX and STCAB beds both have fairly extensive TOS
280 coverage as well *Tribrachidium* of a similar size to those on TBEW. This indicates
281 that the thick mat coverage on 1TT did not prevent the continued growth of the
282 *Tribrachidium* on that bed. Because *Tribrachidium* is not consistently associated
283 with a particular composition of TOS cover, its distribution was not dependent upon
284 a specific kind of organic surface, nor was thick mat cover prohibitive to its growth
285 and survival.

286 The comprehensive description of the different facies represented by Ediacaran-
287 aged beds in South Australia by Droser and Gehling (2013), combined with the *in*
288 *situ* preservation of successive bedding planes, provides a unique opportunity here
289 for analyzing the environmental preferences of these organisms. Importantly, in
290 addition to being found in four of the five facies known from the Ediacaran of South
291 Australia, *Tribrachidium* is the only Ediacara taxon, other than the form genus
292 *Aspidella*, described from South Australia that dominates excavated beds in more
293 than one facies. Because it was able to live in such a diverse array of environments
294 and with a variety of other taxa, *Tribrachidium* can be regarded as an environmental
295 generalist, able to adapt to different physical energies and substrate types. Spatial
296 analyses indicate that *Tribrachidium* on one bed (1TT) was random; however, bed
297 shapes limited spatial analysis to a single bed. Qualitatively, clusters of

Tribrachidium are observed on four of the nine beds bearing *Tribrachidium*. 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.

9.2. *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 groups of similarly-aged individuals. The larger size range and resultant smearing effect of the size frequency distribution 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

320 beds preserve temporally instantaneous “snapshots” of the seafloor with minimal
321 transport (Gehling, 1999; Droser et al., 2006), further supporting the view that
322 *Tribrachidium* populations comprise single generations. Darroch et al. (2013)
323 studied three rangeomorph and one non-rangeomorph taxa, finding that they also
324 showed consistent right-skewed size distributions across different fossil surfaces. In
325 contrast with *Tribrachidium*, the minimum sizes of each genus studied by Darroch et.
326 al. (2013) were equivalent across the different surfaces; hence, the resultant large
327 size range on each surface led them to favor a continuous reproduction model.

328 The distinct size groupings of *Tribrachidium* on individual beds provide insight into
329 the reproductive habits of these organisms. Droser and Gehling (2008) found
330 evidence for sexual reproduction in the Ediacara biota in the presence of
331 synchronous aggregate growth in *F. dorothea*. Populations composed of similarly-
332 sized, and therefore similarly-aged individuals, such as those recorded in
333 *Tribrachidium*, can be indicative of either a seasonal or opportunistic sexual
334 reproductive strategy in modern marine invertebrates. In a seasonal reproduction
335 model, recruitment occurs in seasonal cycles and is commonly triggered by factors
336 such as changes in photoperiod (Young, 2003), and has been observed in several
337 marine invertebrate taxa, including both poriferans and cnidarians (Young, 2003;
338 Conn, 2000). Hellstrom et al. (2010) also describe a coral species that reproduces
339 once annually on a species scale but also on a population scale during different but
340 distinct full moons. Populations of distinct, narrow size ranges can also result from
341 an opportunistic reproductive strategy, whereby environmental factors that are not
342 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).

9.3. 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 preserved ventral morphology of the otherwise characteristic three-armed dorsal aspect of *Tribrachidium*. This is consistent with previous descriptions of *Tribrachidium* that 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. 10). We interpret that the negative external mold is formed when the organism is flipped upside-down prior to or during burial; deposited sand molds the inverted base of the *Tribrachidium*. Conversely, we interpret that 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 have not as yet been observed on any other beds.

There are several explanations for the distribution of positive casts or negative molds on 1TT and TBEW. On 1TT, the *Tribrachidium* specimens 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, namely as casts of pedal impressions. One possibility is that *Tribrachidium* on TBEW were bigger and had therefore been resting overlong on the seafloor; hence, pedal hollows were more likely to form than in the case of the smaller *Tribrachidium* on 1TT. Alternatively, if a small hollow was 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 possible flipping of *Tribrachidium* provides further insight into their ecology. First, flipping seems to be unique to *Tribrachidium*; there are no other known examples, nor is there other evidence of flipping on the excavated Nilpena beds. Second, we find evidence of possible *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.

387 While it seems unlikely that *Tribrachidium* could be flipped in a low-energy
388 environment, such conditions may also have played a role in the preservation of
389 upside-down *Tribrachidium* on the bed. A high-energy environment would have
390 washed organisms away completely after flipping. The lack of other marks such as
391 “mop”, structures of stalks and holdfasts pulled by a current (Tarhan et al, 2010), on
392 the bed near the concentric ridge fossils, particularly the positive impressions, may
393 indicate that *Tribrachidium* was not firmly attached to the substrate. This could
394 explain the presence of concentric ridge fossils on a low energy bed, such as 1TT.
395 Another possibility is that the *Tribrachidium* that were flipped or removed had
396 already died prior to being disturbed. It may be that in life *Tribrachidium* were more
397 firmly attached to the substrate, but after death the attachment was weakened,
398 allowing for easier removal or flipping. The relief of positive features shows that
399 sediment built up around the base of the organism over time, and that
400 *Tribrachidium* was stationary, until moved by environmental forces.

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

Importantly, although the positive concentric ridge features on TBEW superficially resemble *Aspidella*, their size frequency distribution is not right-skewed, as *Aspidella* size frequency distributions have been continuously shown to be (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 (Fig. 11), a feature not reported in *Aspidella*. Considering these factors, the most parsimonious hypothesis is that these concentric ridge fossils are preservations of the base of *Tribrachidium* that result from the removal of the organism. Additionally, the concentric ridge forms on 1TT are negative features, and so do not resemble *Aspidella*.

10. 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 populations composed of single generations. 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 hypothesis 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 biostratinomy 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 lifestyle 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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Figure Captions

Fig. 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. SAM P40941. B-C) *Tribrachidium heraldicum*. SAM P40403; SAM P42662. D) An example of touching *Tribrachidium*. TBEW-108/147; TBEW-108/149. E) A *Tribrachidium* from TBEW in association with micropucker. TBEW-122/134. F) Concentric ridge fossil from 1TT. 1TTA-CC1. G) A 'nestled' concentric ridge fossil, where the relief is the same at the center as at the edge. 1TT-206/176. H) A 'stacked' concentric ridge fossil, where the center ridge has higher relief than the edge. 1TT2-188/-7.

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

Fig. 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).

Fig. 4. 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.

Fig. 5. A plot of the fossils on 1TT. *Tribrachidium* are represented by squares; concentric ridges are represented by triangles. Each box delineated by the grid lines represents one square meter. A photograph of the bed behind the plot shows the shape of the excavated bed. The different symbols show the locations of the fossils on the bed.

Fig. 6. 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 (2015).

Fig. 7. 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.

Fig. 8. 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.

Fig. 9. Size frequency distributions for the *Tribrachidium* and concentric ridge morphology fossils on TBEW and 1TT. The size distribution of concentric ridges on a given bed falls within that of *Tribrachidium* on the same bed.

Fig. 10. 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 may have 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 may have 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. Illustrations by Michelle Kroll.

Fig. 11. A photograph showing faint lines (highlighted by arrows) preserved along the edge of a silly-putty impression of a concentric ridge fossil from TBEW. These lines are not present in *Aspidella*, and may be the preservation of the fringe-like caul observed in *Tribrachidium*. TBEW-FL3c. Scale bar is 1 cm.

Figure 1 Black and White

Figure 1 Color

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6 Color

Figure 7

All Tribrachidium

Selected Beds

Figure 8

Figure 9

Figure 10 Color

Figure 11 Color