A NEW ENIGMATIC, TUBULAR ORGANISM FROM THE EDIACARA MEMBER, RAWNSLEY QUARTZITE, SOUTH AUSTRALIA

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ABSTRACT—Here we reconstruct a new tubular, serially divided organism with a bilateral morphology from the Ediacaran of South Australia. The organism, *Plexus ricei* new genus new species, was a broadly curving tube that resided on the Ediacaran seafloor. *Plexus ricei* individuals range in size from 5 to 80 cm long and 5 to 20 mm wide, and are comprised of two main components: a rigid median tubular structure and a fragile outer tubular wall. *Plexus ricei* is preserved as an external mold on bed soles, and as a counterpart cast on bed tops in sandstones interpreted to represent deposition between storm and fairweather wave-base. The phylogenetic affinities of *P. ricei* are uncertain; *P. ricei* symmetry implies a bilaterian origin, but a lack of defined anterior and posterior ends precludes definitive assignment.

INTRODUCTION

EDIACARA BIOTA fossils offer insight into Earth's oldest macroscopic animals and the earliest complex ecosystems (Narbonne, 1998; Xiao and Laflamme, 2009). While forms such as *Dickinsonia*, *Charniodiscus*, and *Spriggina* are the classic examples of this biota, recent work has shown that fossils of more simple tubular-shaped organisms are in fact the most abundant component of Ediacaran assemblages (Droser and Gehling, 2008; Cohen et al., 2009; Tacker et al., 2010; Sappenfield et al., 2011). While ecological and biological characteristics can be discerned, the taxonomic associations of these tubular fossils remain enigmatic (Droser and Gehling, 2008). Factors that have precluded taxonomic determination of tubular fossils in the past have been: 1) poor preservation of organisms with a tubular construction versus those with a more sturdy construction; 2) the abundance of textured organic surfaces (TOS; Gehling and Droser, 2009), which can resemble densely packed tubular fossils; 3) misidentification of tubular organisms as trace fossils; and 4) the simple morphology of tubular organisms.

Here we reconstruct a new tubular organism from the Ediacaran succession in South Australia. The organism, *Plexus ricei* n. gen. n. sp., is serially divided, has a bilateral morphology, and is dissimilar from any previously described Ediacaran genus or species.

GEOLOGIC SETTING

The field site is on the western margins of the Flinders Ranges, South Australia, which, along with the Mount Lofty Ranges, comprise the Adelaide Geosyncline (Gehling, 2000; Fig. 1). The Neoproterozoic–early Paleozoic strata that make up the geosyncline extend from Kangaroo Island in the south to around 600 km north, and have a combined thickness of more than 20 km (Fig. 2). Deposition of the geosyncline ceased at the onset of the Delamerian Orogeny about 500 Ma (Preiss, 1987). Likely deposited along a passive margin, these strata represent some of the most complete records of mid-to-late Neoproterozoic life (Gehling, 1999; Waggoner, 2003; Gehling and Droser, 2012).

The fossils discussed here occur in the Ediacara Member of the Rawnsley Quartzite. The Rawnsley Quartzite is the youngest part of the Ediacaran Pound Subgroup of the Wilpena Group, which represents a succession deposited during an interval of post-glacial marine transgression (Preiss, 1987). From oldest to youngest, the Pound Subgroup includes the Bonney Sandstone, the Chase Quartzite Member, the Ediacara Member, and the upper Rawnsley Quartzite. The Ediacara Member fills a valley in a landscape unconformity cut into the intertidal sandstone facies of the underlying Chace Quartzite Member of the Rawnsley Quartzite and the Bonney Sandstone, and occurs 50–500 m below a basal Cambrian disconformity (Gehling and Droser, 2009).

There are five sedimentary facies within the Ediacara Member, with the most abundant and diverse fossil assemblages occurring in laterally continuous, ripple-topped sandstone beds of the Wave-Base Sand Facies (Gehling and Droser, 2013; Fig. 3). This facies represents deposition between fairweather wave-base and storm wave-base. Beds range in thickness from less than 1 cm to 30 cm and are medium- to coarse-grained. The soles of these beds contain the molds of the soft-bodied Ediacara biota, including *Plexus ricei* n. gen. n. sp. Trace fossils and microbial mat-associated TOS are also preserved along bed interfaces (Gehling, 1999, 2000). *Plexus ricei* additionally occurs in the sheet-flow sand facies consisting of laterally continuous, medium- to coarse-grained event beds with tool marks and planar laminations (Gehling and Droser, 2013).

Taphonomy of the Ediacara biota.—Fossils of the Ediacara Member occur as external molds and casts on the bases of beds in relatively coarse-grained quartzite successions. At our field site, molds and casts occur in negative and positive hyporelief on bed soles.

Organisms were molded and cast by sand that smothered communities in situ; fossils are not stretched, folded, ripped, nor do they exhibit preferred orientations, all evidence that would imply transport before burial (see Gehling and Droser, 2013). Counterparts of original casts and molds can be found on the tops of underlying beds.

Two categories of preservation reflect the anatomy of the original organism. First category: after burial, the majority of taxa, including forms such as *Dickinsonia*, *Spriggina*, *Coronacollina*, and *Tribrachidium* resisted collapse and the overlying sand molded their positive-relief bodies. Second category: forms such as *Phyllozoon* collapsed upon burial. During early diagenesis decaying organisms would form a mineralized crust, or "death
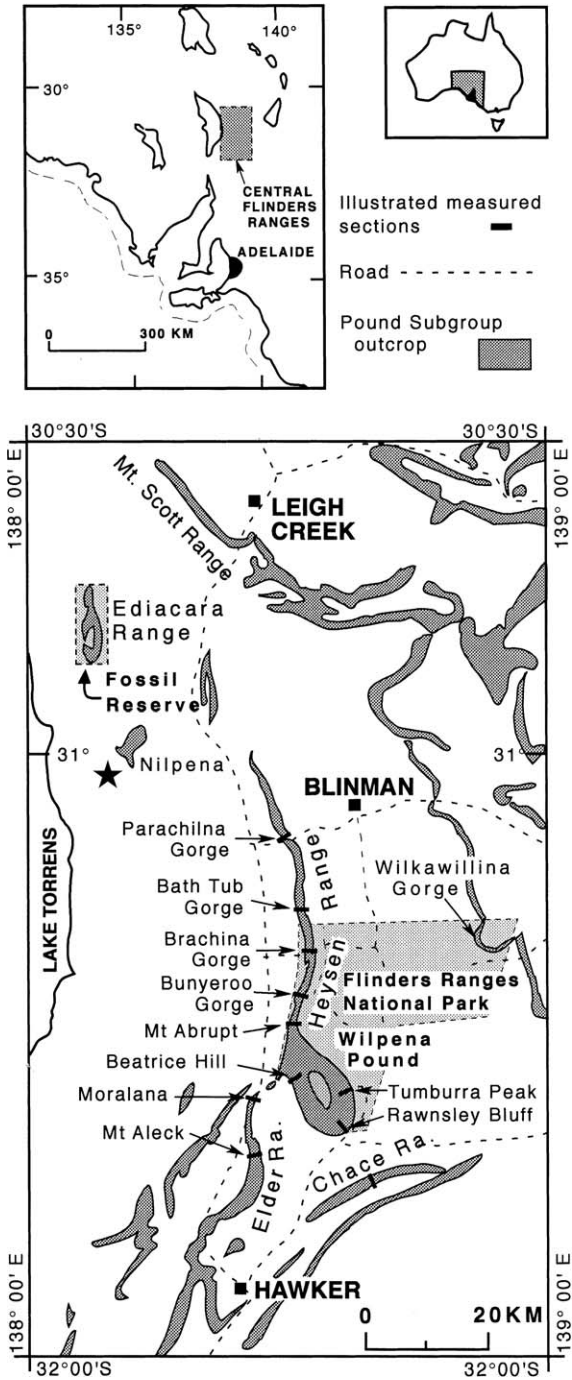
FIGURE 1—Flinders Ranges locality map, Nilpena field site marked by star (after Gehling, 2000).

FIGURE 2—Terminal Proterozoic and Cambrian stratigraphy of the Flinders Ranges, South Australia (after Gehling and Droser, 2012).

mask" sole veneer associated with the decaying organisms, formed in the overlying, still-unconsolidated sediment (Gehling, 1999). This means the molds of uncollapsed organisms like *Dickinsonia*, in an unbioturbated substrate, would have persisted following organism decay. Unconsolidated underlying sand subsequently cast the now-consolidated mold. Conversely, organisms which had collapsed immediately upon burial, such as *Phyllozoon*, formed similarly-mineralized molds in the underlying sand, and were subsequently cast by overlying burial sands following organism decay. In the field, on bed soles, these
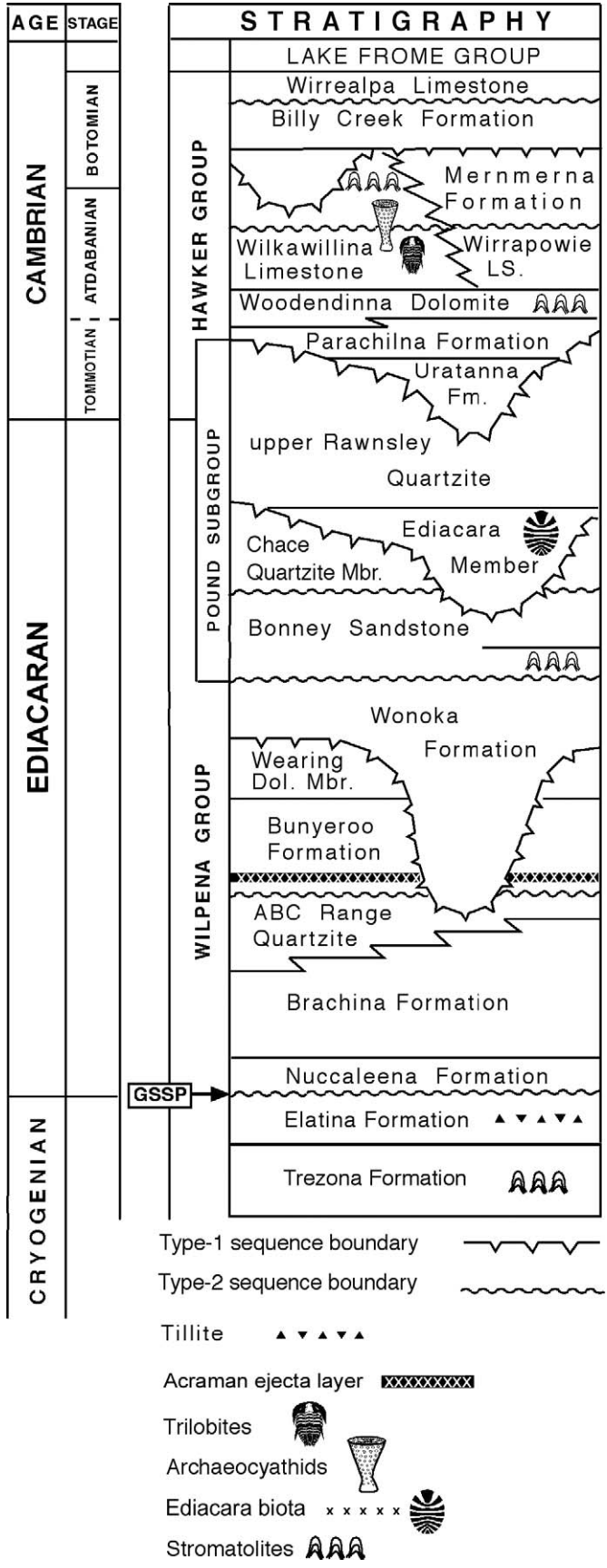
1. Shoreface Sands

2. Wave-Base Sands

Rawnsley Quartzite

Ediacara Member

Chace Quartzite Member

Bonney Sandstone

Fairweather wave base

Storm wave base

3. Delta-Front Sands

Intertidal Mat Sands

Fluvial Deltaic Sands
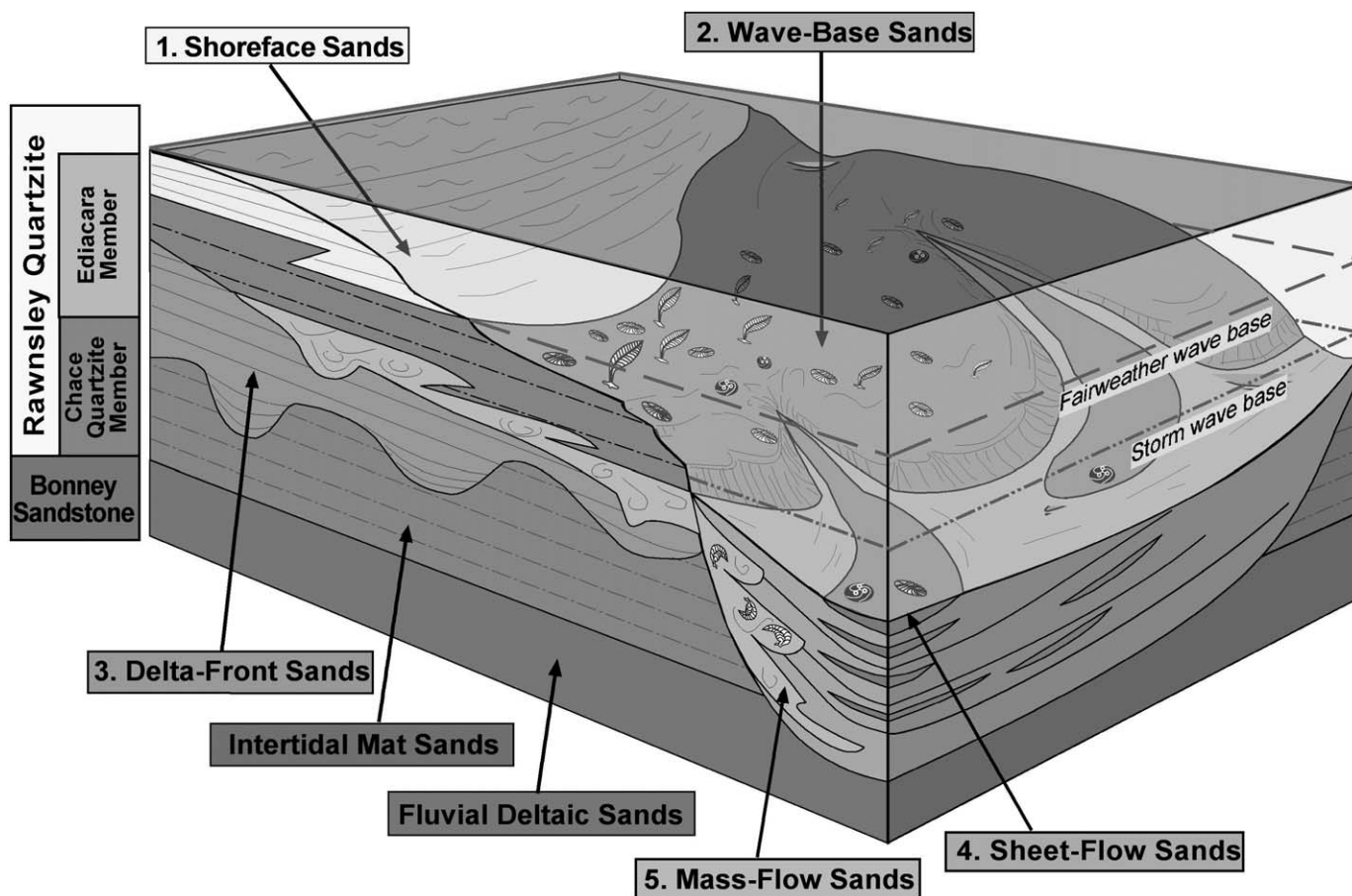
5. Mass-Flow Sands

4. Sheet-Flow Sands

FIGURE 3—Diagram illustrating the five main sedimentary facies of the Ediacara Member (after Gehling and Droser, 2013): *1*, shoreface sands; *2*, wave-base sands; *3*, delta-front sands; *4*, sheet-flow sands; *5*, mass-flow sands. The two facies discussed here are the sheet-flow sands and the wave-base sands.

unique molds and casts occur in negative and positive hyporelief, respectively.

MATERIALS AND METHODS

All fieldwork and excavations occurred at the National Heritage Listed Ediacara fossil site at Nilpena, where systematic excavation of fossiliferous beds has been carried out over the past ten years. Because South Australian Ediacara fossils are best preserved on bed soles, in-place beds are traced onto a sheet of transparent plastic and, upon excavation, inverted and reassembled in a nearby, cleared area. The traced plastic sheet is used as a map for bed reconstruction. At Nilpena, 30 fossil-bearing beds have been excavated, exposing over 200 m² of bedding surface area. Beds are divided into 50 cm² grids, and all bedding plane structures are logged for analysis.

Plexus ricei n. gen. n. sp. was examined on the soles and tops of excavated bedding horizons and on pieces of float. The lengths of individual *P. ricei* specimens were measured using a string ruler divided into centimeter intervals, and widths were measured using digital calipers capable of measuring to the nearest hundredth millimeter. Latex molds were made of *P. ricei* bed sole specimens. The distribution and orientation of *P. ricei* between and within different excavation sites were also documented. The holotype, paratype, and other figured specimens are at the Nilpena and Ediacara Conservation Park field sites, and in the collections of the South Australian Museum (SAM).

Plexus ricei *field excavation sites.*—*Plexus ricei* has not been described from any deposits outside of those at Nilpena. The two *P. ricei* Nilpena excavation sites described here include a series of beds found within the sheet-flow sand facies (Beds Mount Michael Tribrachidium, Mount Michael Sub, and Mount Michael Sub-Sub, abbreviated here as MMTB, MMS, and MMSS), and a series within the wave-base sand facies at the Plinth site (Plinth Beds PBA, PBB, PBC, and PBD). *Plexus ricei* occurs as a mold on all bed soles at both sites.

SYSTEMATIC PALEONTOLOGY

PLEXUS new genus

Type species.—*Plexus ricei* new species, by monotypy.
Diagnosis.—As for type species.
Etymology.—From the Latin *plexus* for braid, or plait; assigned based on reconstruction of fossil as a serially divided organism.
Occurrence.—Ediacara Member, Rawnsley Quartzite, South Australia.

PLEXUS RICEI new species
Figures 4.1–4.5, 5.1–5.3, 8, 9

Diagnosis.—Broadly looping, self crossing, 5–20 mm wide and 5–80 cm long serially divided outer tubular wall with median tubular structure. No clear anterior and posterior polarity. Occurs as loops 6–10 cm wide and 8–16 cm long.
Description.—*Plexus ricei* n. gen. n. sp. is preserved as an external mold on bed soles (Figs. 4.1, 4.5, 5.2, 5.3), and as a counterpart cast on bed tops (Figs. 4.2–4.4, 5.1). External molds
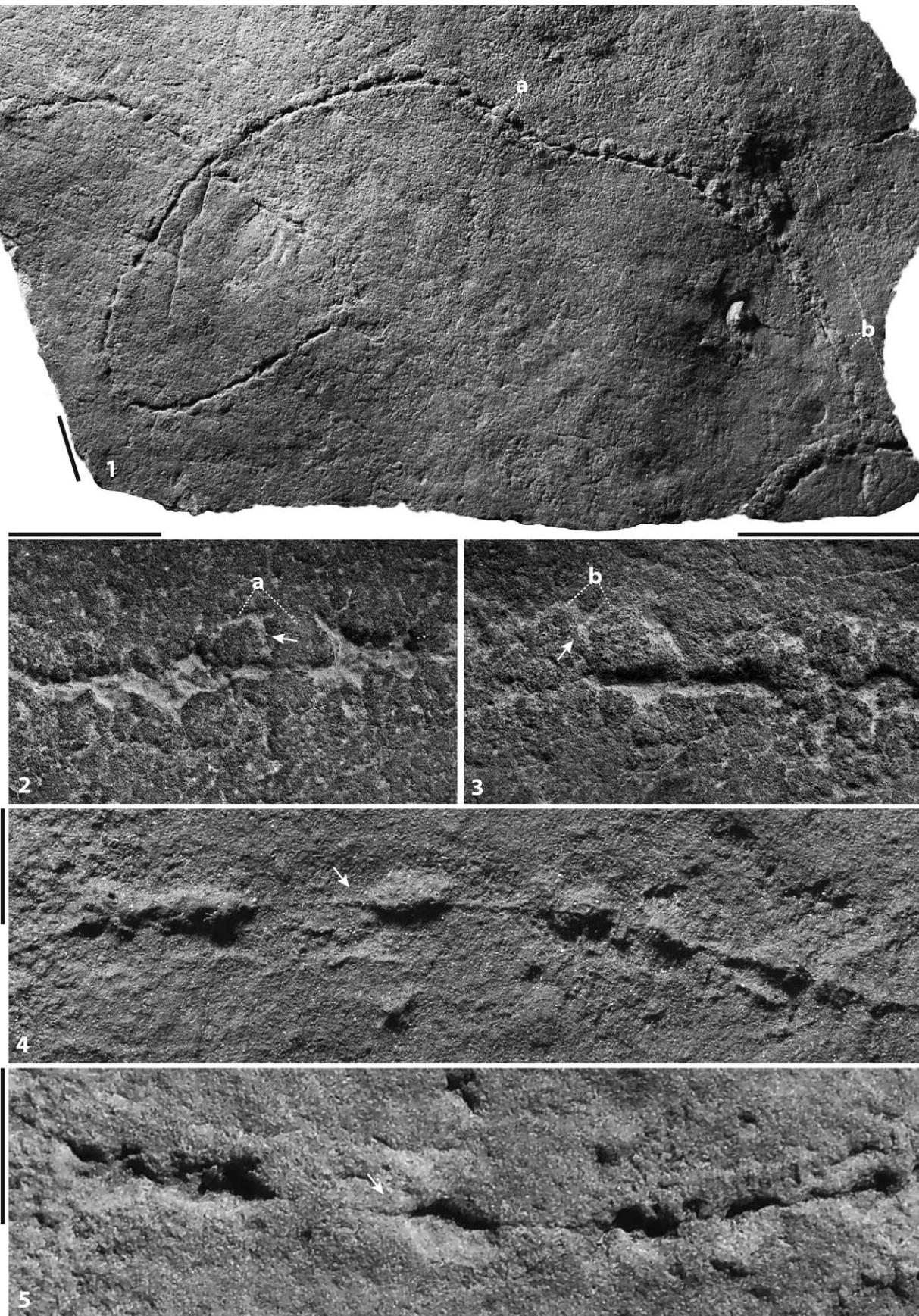
FIGURE 4—*Plexus ricei* (*1* is a bed sole specimen, *2* and *3* are latex molds of *1*, *4* is a latex mold of *5*): *1*, (SAM P47812), holotype, note median negative groove, positive peripheral berms (dashed lines at a and b), and bilateral symmetry; labels a and b correlate to *2* and *3*; *2*, latex mold of *1* at a; note serial divisions
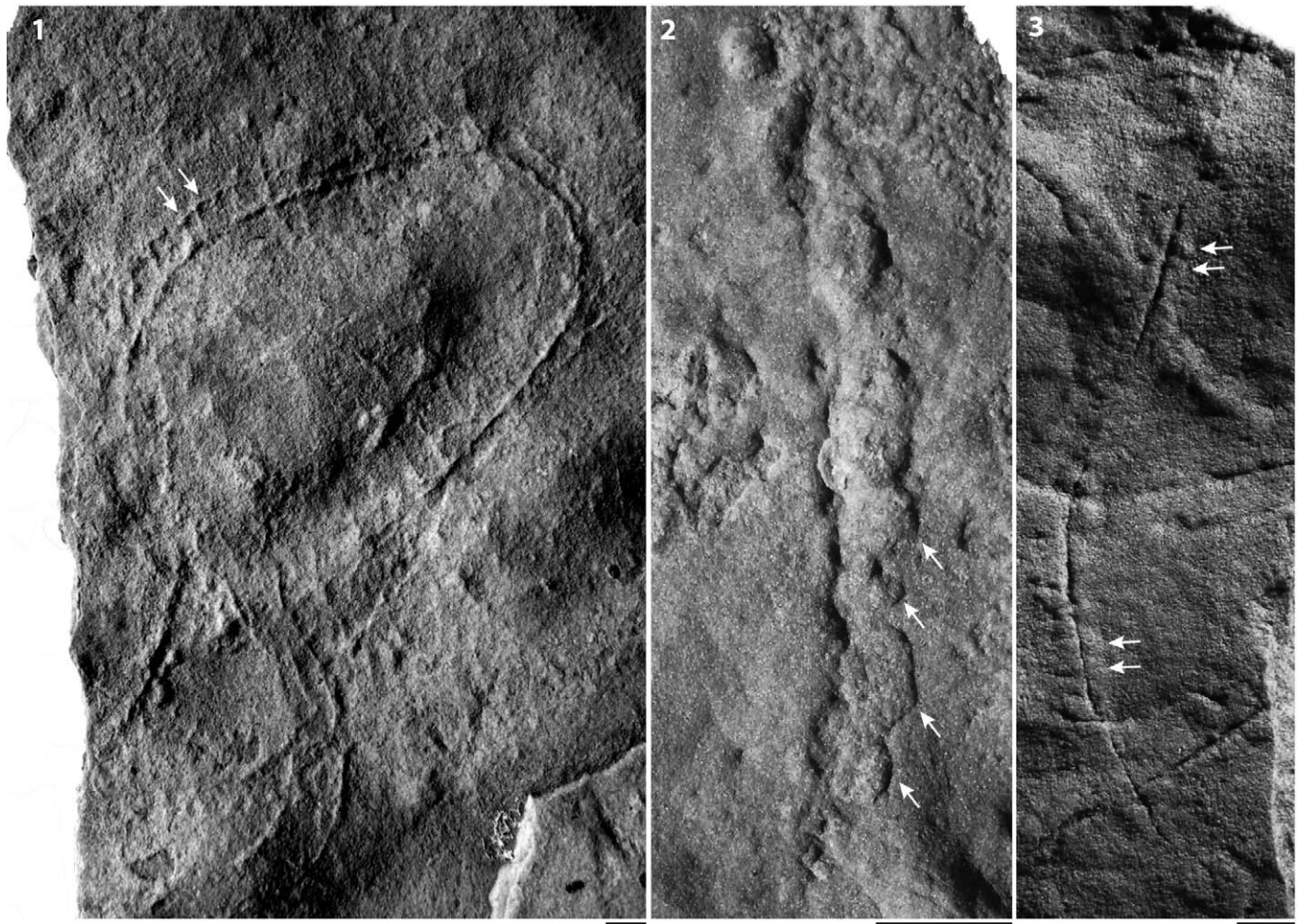
FIGURE 5—*Plexus ricei. 1,* (SAM P35700b), positive epirelief bed top specimen; note broad looping and serial divisions (unmarked arrows); *2,* (MMSS-2), MMSS bed sole specimen; note berm and serial divisions preserved on one side of groove (unmarked arrows), and sharp berm-rock boundary; *3,* (SAM P47816), bed sole specimen; note discontinuous nature of groove and serial divisions (unmarked arrows). Scale bar=1 cm.

consist of a negative hyporelief median groove flanked by positive hyporelief berms (Figs. 4.1, 5.2, 5.3). Groove widths range both among individuals and within individuals (Fig. 6); variability in width is typically greater between rather than within individuals. The holotype (Fig. 4.1–4.3) is 57 cm long, and has 0.5–3 mm-wide grooves. Total width, encompassing both grooves and berms, may vary on the order of several millimeters (5–20 mm) between individuals. Grooves are shallow, never exceeding a few millimeters in depth.

Groove diameters were measured at regular two-millimeter intervals along the lengths of several specimens (Fig. 6). Groove diameters in a single *P. ricei* specimen can vary from, for example, 1 to 3.5 mm; diameters of measured specimens may fluctuate or vary: individual grooves widen and then taper (Fig. 4.4, 4.5). Total groove and berm widths were not always measured because most berms are very poorly preserved when present.

Margins between *P. ricei* grooves and berms are sharp. Outside edges of berms are also sharp, with no gradient between the fossil and the surrounding matrix (Fig. 5.2). Berms are separated into commonly oval, paired divisions divided by the median groove.

The boundaries where two divisions meet are perpendicular to the *P. ricei* central axis. Division size is consistent within a single specimen. Between specimens, though, division size may vary. The holotype (Fig. 4.1–4.3) has a division pair 5 mm long along the central axis and 10 mm wide perpendicular to the central axis. Other specimens (Fig. 5.1, 5.3) have pairs that are 5 mm by 15 mm and 2 mm by 7 mm along the same dimensions.

Etymology.—Latinized *ricei* for Dennis Rice, Honorary Associate of the South Australian Museum.

Types.—Holotype, SAM P47812; paratypes, SAM P35700b, SAM P47816.

Occurrence.—Ediacara Member, upper Rawnsley Quartzite, National Heritage Listed Ediacara fossil site at Nilpena and Ediacara Conservation Park.

Remarks.—*Plexus ricei* is identified by its central groove and, where preserved, its berms. While variation exists among specimens, *P. ricei* varies more greatly from other tubular Ediacara genera: *Somatohelix sinuosus* (Sappenfield et al., 2011), while also curving and elongate, lacks the characteristic *P. ricei* serial divisions. *Funisia dorothea* (Droser and Gehling, 2008), while serially divided, lacks the *P. ricei* groove.

←
(dashed lines) and positive ridge separating divisions (unmarked arrow); *3,* latex mold of *1* at b; note transverse ridge dividing berms into units (unmarked arrow); *4,* latex mold of *5*; note tapering median ridge (unmarked arrow, corresponds to arrow in *5*); *5,* (MMSS-1), negative MMSS bed sole specimen; note tapering median groove (unmarked arrow). Scale bar for *1*=2 cm, Scale bar for *2–5*=1 cm.
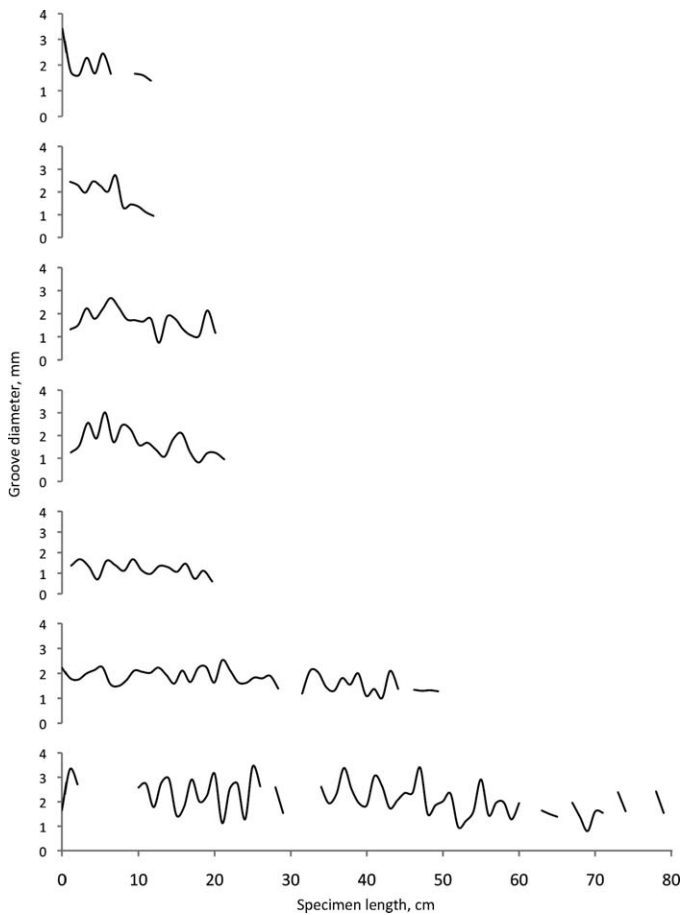
FIGURE 6—Diametric fluctuations within seven separate *Plexus ricei* individuals. Horizontal axis is specimen length in centimeters; vertical axis is groove diameter in millimeters. Note widening and tapering along individual lengths.

PRESERVATION AND RECONSTRUCTION

Plexus ricei n. gen. n. sp. occurs as a part and counterpart. Bed sole molds have corresponding casts on underlying bed tops. Like most fossils at Nilpena, the best-preserved *P. ricei* specimens occur as bed sole molds. Median tubular structures resisted collapse along some portions of the lengths and collapsed along others, forming the commonly irregular bed sole grooves. Groove molds formed when relatively rigid median tubular structures resisted collapse, and berms formed when relatively fragile outer tubular walls collapsed. Following decay, mineralization ensued during early diagenesis, proceeded by casting of the molds by underlying sediment (Fig. 7). Collapsed lengths are not coincident with serial divisions. Outer tubular walls always collapsed, forming bed sole berms. Median tubular structures of larger specimens were more resistant to collapse; this explains why grooves wider than 5 mm are commonly continuous. Collapsed portions are comparable to other collapsed Ediacaran tubes such as *Phyllozoon* (see Gehling et al., 2005).

Plexus ricei berm boundaries are sharp, implying well-defined organismal margins (Fig. 5.2). Also, sharp berm-groove boundaries imply little to no tissue between median tubular structures and outer tubular wall margins (Fig. 7); if any significant amount of tissue existed in this space, the berm-groove boundary would be gradual. Serial division boundaries, like grooves, occur in negative hyporelief, indicating a level of

margin rigidity (Fig. 7.5a); margins between divisions are perpendicular to the lengthwise axis of *P. ricei*.

Plexus ricei molds and casts curve and commonly loop, overlapping themselves or other *P. ricei* specimens. Unlike trace fossils, individual tubes do not crosscut one another. Instead, one individual overlaps another individual or itself. While the curving nature of *P. ricei* indicates the organism was flexible, it is unclear if looping is an original characteristic or a biostratinomic artifact.

It is not clear whether any complete *P. ricei* specimens were observed—even the longest specimen (80 cm) does not have ends that can be identified as anterior or posterior. Still, when it occurs, *P. ricei* is consistently preserved along its length, so either specimen termini are rarely preserved, or termini are not unique (for instance, specimens end without features that are remarkably different from the rest of the organism). Where lengths appear to terminate, it is unclear if it is the result of taphonomy or original anatomy.

Plexus ricei was an epibenthic, tubular, serially divided organism with a bilateral morphology (Fig. 9). *Plexus ricei* likely did not stand erect within or on top of the sediment, as suggested by the lack of evidence for foundational support structures, and the fossil's general lack of orientation on several bedding planes (e.g., all Plinth site beds); an organism anchored to the substrate and suspended in the water column should, upon burial, be preferentially oriented in the direction of the final, pre-burial current(s) (see Droser et al., 2005). Likewise, there is no trace fossil associated with *P. ricei*, so the organism is assumed to have been sessile. While *P. ricei* may have been planktonic, this is unlikely due to the fossil's complete absence on other rippled beds similar to those at the Plinth site and in the sheet-flow sand facies bed series; if *P. ricei* were planktonic, then it should occur ubiquitously within the facies that it is preserved.

Plexus ricei at Nilpena.—*Plexus ricei* is poorly preserved on the soles of all Plinth site beds (berms are rarely preserved, for example), though preservation is sufficient to distinguish among individual grooves. *Plexus ricei* is pervasive on the soles of PBA and PBB, but appears to become more sparse on PBC and PBD. *Plexus ricei*-bearing float is very common in the vicinity of the Plinth site.

Plexus ricei is less common on sheet-flow sand facies beds and is commonly preserved in this facies in greater detail than at the Plinth site. The longest *P. ricei* recorded (80 cm) occurs on MMTB. MMS grooves have small widths compared to MMTB and MMSS grooves (for instance, one MMS groove is 0.5–1.5 mm wide, compared to the 1–4 mm widths of the 80 cm MMTB specimen). The most detailed *P. ricei* specimens observed in the field are on MMSS. One MMSS berm occurs only on one side of and is more than three times as wide as the central groove (Fig. 5.2). MMTB and MMSS preserve clear TOS, which uncommonly overlap *P. ricei*.

The preservational quality of *P. ricei* is thus facies-specific. Specimens are best preserved in the sheet-flow sand facies bed series, which are finer-grained than Plinth beds. The *P. ricei* berm is very rarely preserved on Plinth bed soles. Presumably, the coarser-grained Plinth beds inhibited detailed preservation of the organism. Each facies, then, presents *P. ricei* in a different taphonomic grade. There is no apparent correlation between primary sedimentary structures and *P. ricei* distribution; Plinth specimens occur both at the crests and troughs of ripples. Nor does *P. ricei* distribution appear to correlate with bed thickness, as specimens occur both on the soles of beds that are less than 1 cm thick, and on the soles of 12 cm-thick event beds.
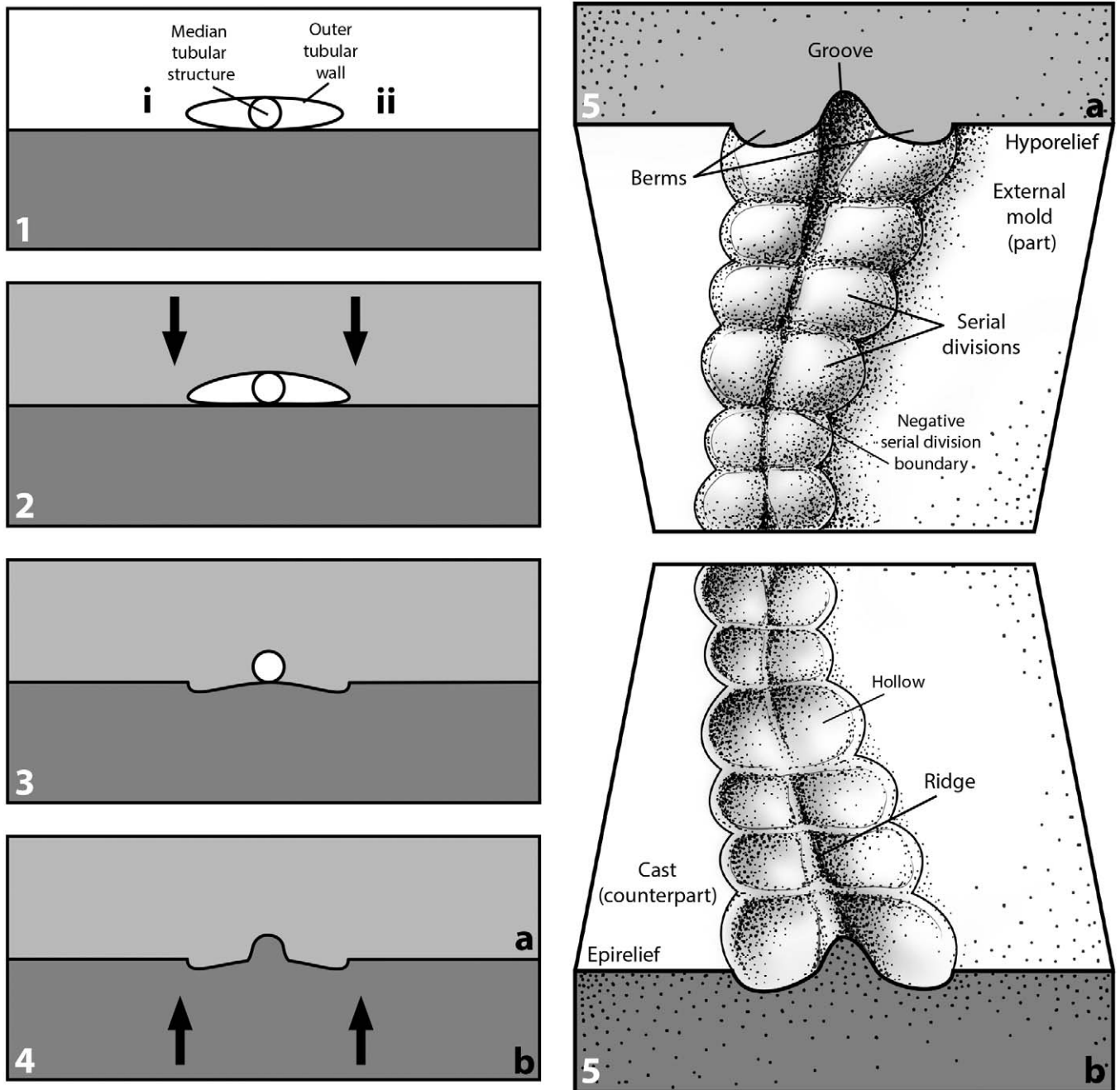
FIGURE 7—*Plexus ricei* taphonomy. *1*, pre-burial; note i–ii cross-section transect (see Fig. 9); note lack of vertical space between median tubular structure and outer tubular walls; *2*, immediately post-burial; note compacted outer tubular walls; *3*, post-burial; rigid median tubular structure persists, fragile outer tubular walls collapse, decay ensues; *4*, decay of median tubular structure proceeds, mineralization of sole veneer death mask binds external mold; unconsolidated underlying sediment casts mold; *5*, *P. ricei* external mold part (a) and external cast counterpart (b).

PALEOECOLOGY

Plexus ricei, "Aulozoon", and *Aspidella* are preserved repeatedly on stratigraphically successive beds at the Plinth site; such a repetitive preservational pattern is unique among the fossil beds at Nilpena (see Droser et al., 2006). Rounded wave-crest ripples, sharp interstratal contacts, and coarse grains indicate deposition above storm but below fairweather wave-base (Gehling and Droser, 2013). The lack of preferred orientation among *P. ricei* specimens implies limited reworking and transport prior to burial. Plinth site beds, then, preserve a relatively dense community of organisms that repeatedly inhabited a specific depositional environment.

There are more *P. ricei* per unit area on Plinth site beds than there are on the sheet-flow sand bed series, in spite of the greater preservational fidelity and thus higher likelihood of preservation of the latter. This implies the distribution of *P. ricei* at Nilpena is non-uniform and non-random, with Plinth site beds representing the maximum *P. ricei* fossil occurrence. While absolute population sizes cannot be reliably estimated, we suggest *P. ricei* proliferated in higher energy depositional settings above storm wave-base. It is unclear how *P. ricei* may have anchored
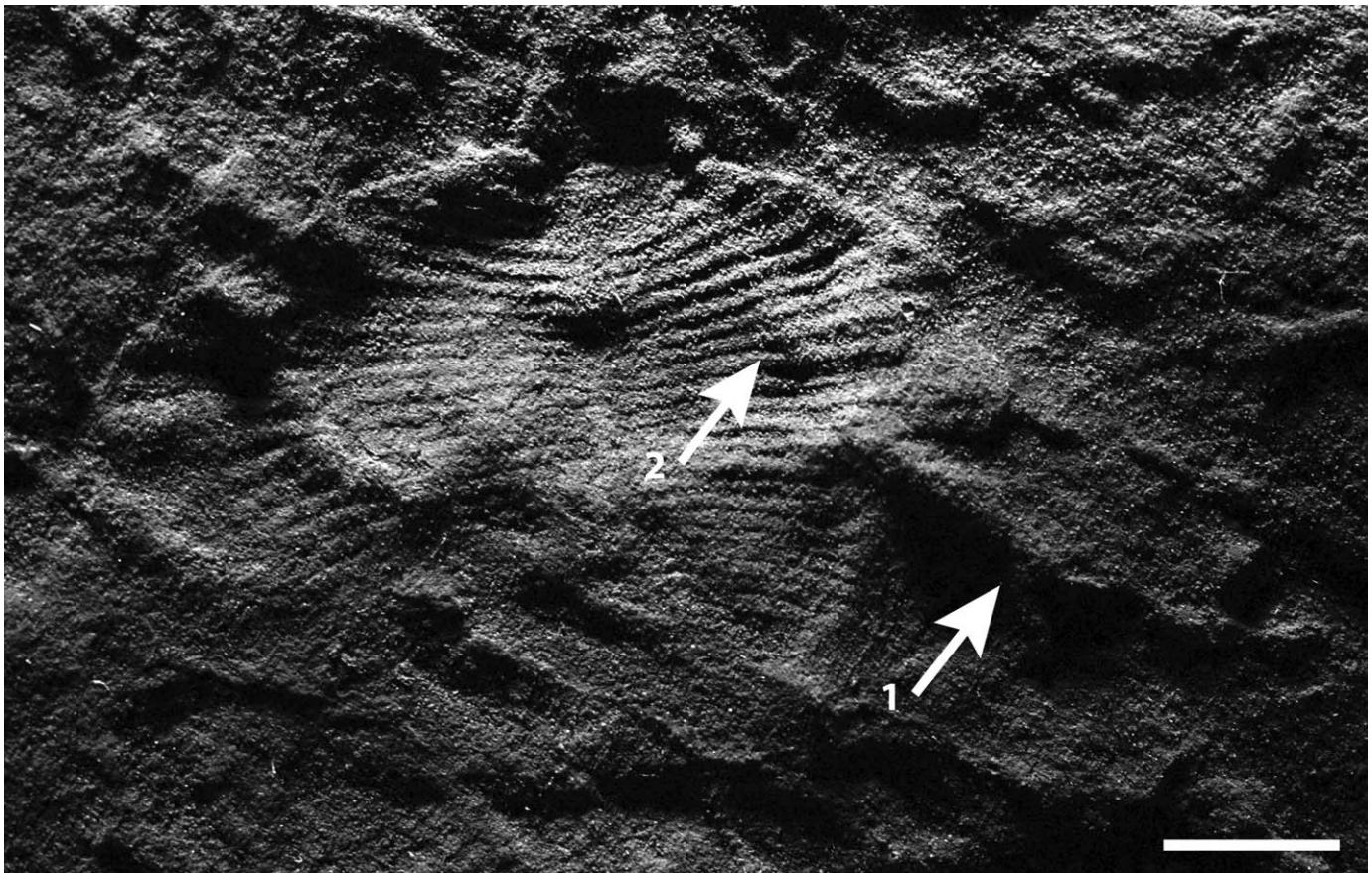
FIGURE 8—Latex mold of bed sole *Dickinsonia* (SAM P42080) and *Plexus ricei* (SAM P44338) external molds. *Plexus ricei* borders *Dickinsonia* (arrow 1); *P. ricei* mold underlies *Dickinsonia*, "pushing up" and distorting *Dickinsonia* ridges (arrow 2) rather than cutting it. Scale bar=1 cm.

itself to the substrate; we conjecture that the serially divided outer tubular wall may have helped *P. ricei* adhere to the sediment, as serial divisions could have provided added traction.

PLEXUS RICEI AFFINITIES

Plexus ricei is not a trace fossil.—*Plexus ricei* n. gen. n. sp. is trace fossil-like, but several observations clearly negate a trace fossil origin.

Plexus ricei is rarely preserved in direct contact with other Ediacaran organisms. Notably, though, one specimen is preserved with and underlies a single *Dickinsonia* fossil on the sole of a float piece (Fig. 8); here the characteristic ridges of *Dickinsonia* imprint through the *P. ricei* groove. For such an imprint to occur, *Dickinsonia* had to have overlain *P. ricei* on the seafloor before burial. *Plexus ricei* pushed up as a result of burial pressure through *Dickinsonia* after both organisms were buried, forming a *Dickinsonia* ridge-imprinted groove. If *P. ricei* were a trace fossil, then the groove would cut through *Dickinsonia*. This imprint relationship is similarly observed where two *P. ricei* specimens intersect: when the two lengths come into contact, one specimen overlaps the other instead of cross-cutting.

The Ediacaran trace fossil *Helminthoidichnites*, first described by Glaessner (1969) as Form B, is common at Nilpena. *Helminthoidichnites* is unequivocally a trace fossil. Although *P. ricei* looks superficially like a trace fossil, it does not fulfill the same ichnofossil criteria as *Helminthoidichnites*.

The levee-lined, millimeter-scale furrows of *Helminthoidichnites* have guided meander morphology, exhibit consistent diameters within individual specimens, and are preserved primarily on the soles of very thin beds in both positive and negative hyporelief. *Helminthoidichnites* is pervasive on the soles of beds less than 10 mm thick, but is extremely rare on beds greater than 10 mm and less than 20 mm thick. *Helminthoidichnites* is entirely absent from the soles of beds greater than 20 mm thick; within an individual bed of varying thickness, *Helminthoidichnites* is invariably restricted to thinner portions.

Plexus ricei, conversely, occurs on the soles of event beds as thick as 12 cm (MMS, for instance). *Plexus ricei* cannot be a trace fossil because, for a negative relief trace fossil to exist on the sole of a thick event bed, the trace fossil constructor first had to have mined down to that sedimentary layer. For *Helminthoidichnites*, in contrast, the thicknesses of beds likely represent the bed thickness the trace fossil constructor had to mine through. Moreover, with vertical bioturbation absent in Ediacaran rocks (see Jensen et al., 2006), a trace fossil origin for *P. ricei* becomes exceedingly unlikely.

Plexus ricei berms resemble levees, which could be evidence for sedimentary displacement by a trace fossil constructor. However, many specimens have berms that are several times as wide as the central groove. For example, a groove on the holotype specimen is 1 mm wide, whereas the surrounding berm is 7 mm wide (Fig. 4.2). This precludes a trace fossil origin for *P. ricei*, as the volume of displaced sediment should be proportional to the size of the trace fossil constructor.

Many *P. ricei* grooves exhibit a range of diameters along their lengths (Fig. 6); trace fossil diameters should be consistent throughout their length and only widen at turns (Ekdale et al., 1984; Droser et al., 2005). In contrast, several straight *P. ricei* grooves widen and contract along their lengths. Well-preserved
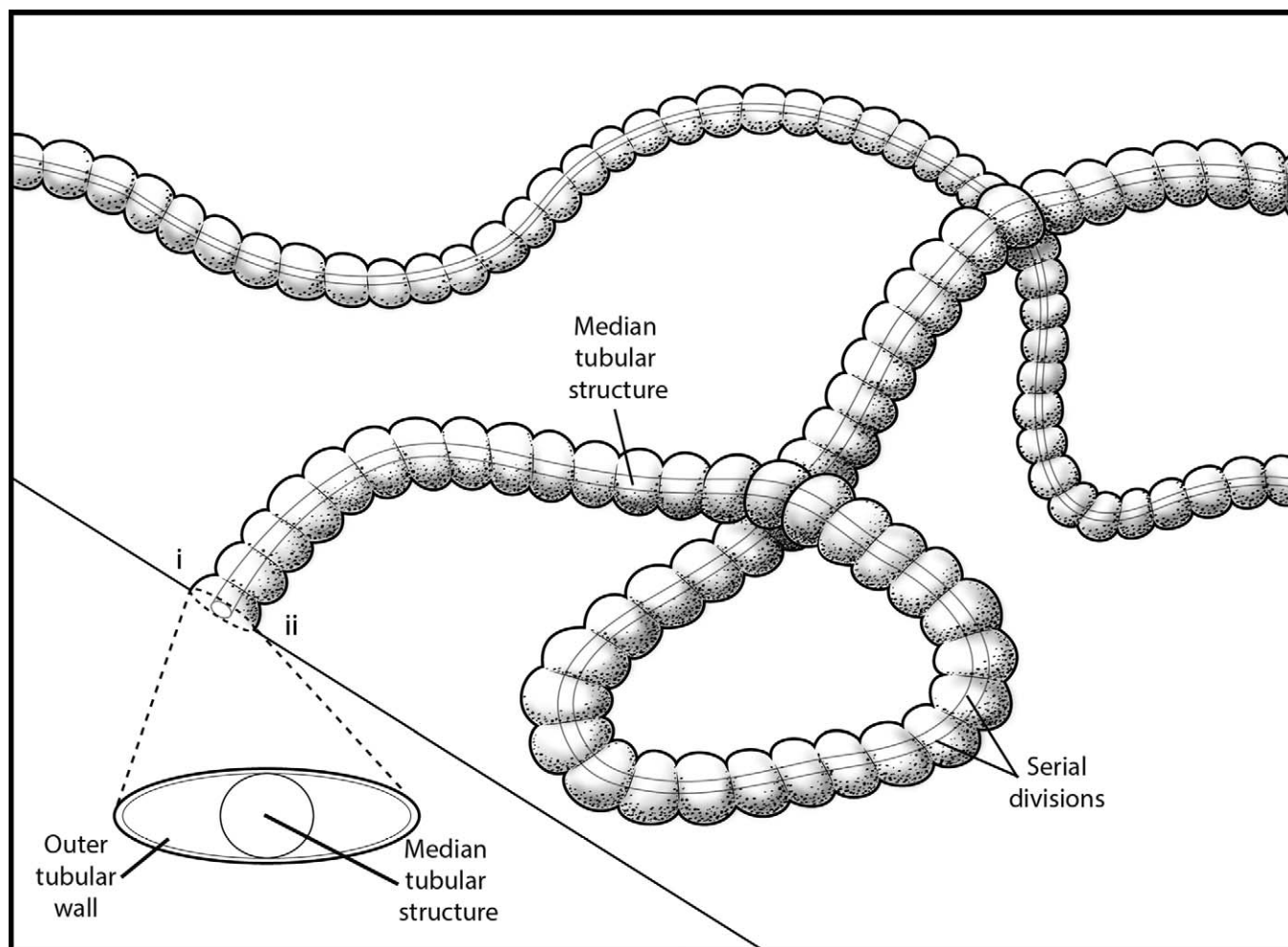
FIGURE *9—Plexus ricei* reconstruction. Note i–ii cross-section from Figure 7, serial divisions, looping, median tubular structure, and outer tubular walls.

specimens reveal that *P. ricei* diameters fluctuate because berms gradually and abruptly "envelop" or "open" around grooves. Finally, while trace fossil diameters can decrease where an intrastratal trace fossil intersects another stratum, this does not explain why some *P. ricei* berms continue to be preserved even when the main groove has disappeared.

Possible bilaterian origin for P. ricei.—*Plexus ricei* is bilaterally symmetrical along its central axis. Coelomate and acoelomate bilaterians generally have a complete, through-going digestive tract; the through-going median tubular structure of *P. ricei* may represent bilaterian-grade digestive tissue. Assigning *P. ricei* to a group, though, is difficult due to the lack of phylogenetically diagnostic anatomical information. Still, because the kind of rigid tissue that molded the *P. ricei* groove is not known in described Precambrian algal and algal-like specimens (see Xiao et al., 2002), an algal affinity for *P. ricei* cannot be confidently assigned.

The origin of the *P. ricei* median tubular structure preserved as a groove mold is unclear. Some modern annelids are detritivores (e.g., *Aeolosomoa*), and so it is possible that the central groove is the mold of ingested detritus resisting compaction upon burial. Thin section petrography, however, provides no support for this: if the tubes are the molds of ingested material, then in thin section there should be an unconformity between the grains of the positive *P. ricei* ridges (which, in this scenario, are composed of the ingested material that molded the grooves) and the grains of the rest of the sample. No such unconformity is present.

CONCLUSIONS

Plexus ricei is a new, serially divided, bilaterally symmetrical Ediacaran organism. Incomplete preservation—particularly of the anterior and posterior ends of the organism—prevents definitive assignment of *P. ricei* to any known group. Identification of *P. ricei* as a non-trace fossil, however, is an important step toward refining the Ediacaran trace fossil record, which represents the only definitive fossil evidence for the appearance of the earliest motile bilaterians.

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