A mixed Ediacaran-metazoan assemblage from the Zaris Sub-basin, Namibia

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ABSTRACT

It has been proposed that the terminal Neoproterozoic Ediacara biota were driven to extinction by the evolution of metazoan groups capable of engineering their environments (the ‘biotic replacement’ model). However, evidence for an overlapping ecological association between metazoans and soft-bodied Ediacaran organisms is limited. Here, we describe new fossil localities from southern Namibia that preserve soft-bodied Ediacara biota, enigmatic tubular organisms thought to represent metazoans, and vertically-oriented metazoan trace fossils. Although the precise identity of the tracemakers remains elusive, the structures bear several striking similarities with the Cambrian-Recent ichnogenus *Conichnus*. These new data support inference of stratigraphic and ecological overlap between two very different eukaryotic clades, and indicate the existence of unusual ecosystems comprising both Ediacara biota and metazoans immediately prior to the Cambrian explosion.

Keywords: Ediacaran; Cambrian; metazoans; trace fossil; ecosystem engineering; *Conichnus*, *Shaanxilithes*, *Aspidella*

1. Introduction

The terminal Neoproterozoic (Ediacaran; 635 – 541 Ma) Ediacara biota is an enigmatic assemblage of large, morphologically complex eukaryotes. The biological affinities of the Ediacara biota are controversial (Xiao and Laflamme, 2009; Laflamme et al., 2013), however it is likely that most groups represent multicellular eukaryotes that went extinct prior to the Cambrian radiation of bilaterian metazoans. With the exception of a few isolated occurrences (Jensen et al., 1998; Hagadorn and Waggoner, 2000), Ediacara-type fossils are largely absent from Cambrian and younger strata despite favorable preservational settings (Buatois et al., 2014). To account for this extinction event at the end of the Ediacaran, Laflamme et al. (2013) proposed a ‘biotic replacement model’ whereby early members (or precursors) of the Cambrian evolutionary fauna gradually displaced Ediacaran biotas through a combination of predatory displacement (see also Seilacher, 1992; Bengtson and Yue, 1992; Hua et al., 2003) and ecological engineering of Ediacaran-type ecosystems. The ‘biotic replacement’ model for the end of the Ediacara biota therefore predicts a protracted Ediacaran turnover involving significant stratigraphic overlap between soft-bodied Ediacara biota, and organisms more typical of the Cambrian evolutionary fauna (Seilacher, 1992; Laflamme et al., 2013; Schiffbauer et al., in press).

Despite this hypothesized lengthy overlap of Ediacaran macrobiota and metazoan ecosystem engineers, few sites preserve fossil evidence for co-occurrence of these groups. Instead, review of older (i.e., ‘White Sea’ assemblage) Ediacaran sections suggests a different scenario, in that direct (i.e., same bed or same slab) associations

between Ediacara biota and metazoans are almost universally rare (see Chen et al., 2014 for a possible exception). This is in part due to careful specimen-based work that has led to re-descriptions of many Ediacaran ‘trace-fossils’ in pre-Nama assemblages as body fossils (see Jenson et al., 2005; 2006; Sappenfield et al., 2011), such that *Helminthoidichnites* is the only trace fossil from this interval still universally viewed as representing a metazoan (and specifically bilaterian) tracemaker. Here, we describe new fossil localities from the youngest Ediacaran strata in southern Namibia that preserve Ediacara biota, enigmatic tubular organisms thought to represent metazoans, and vertically oriented trace fossils characteristic of Cambrian-type metazoan activity.

2. Geological Setting

The Nama Group in southern Namibia is divided into two sub-basins separated by a paleo-topographic high. The Proterozoic to Cambrian-aged Nama Group (Schwarzrand Subgroup) forms a mixed siliciclastic-carbonate succession deposited in a foreland basin on the western and northern margins of the Kalahari craton (Germs, 1983; Grotzinger et al., 1995; Saylor et al., 1998; Vickers-Rich et al., 2013). Regionally, the Schwarzrand Subgroup is underlain by mixed carbonate and clastic sediments of the Kuibis subgroup, which includes microbial-metazoan reef complexes (Grotzinger et al., 2000; Penny et al., 2014). Overlying Schwarzrand strata record subsequent regional shallowing, and are composed of shales, siltstones, and sandstones representing deposition in a range of tide- and delta-influenced shoreface environments (Germs, 1983; Grotzinger et al., 1995; Saylor et al., 1998).

There are few geochronological constraints for the Schwarzrand Subgroup in the Zaris sub-basin, although coeval sections from the Spitzkopf Formation are dated as Ediacaran in the southern Witputs sub-basin (545 ± 1 Ma – Grotzinger et al., 1995). An ash bed from the underlying Kuibis Subgroup (Hoogland Member) in the vicinity of our sites yields a U-Pb zircon age of 548.8 ± 1 Ma (Grotzinger et al., 1995) and so gives a maximum age for the Schwarzrand (Figure 1). The overlying Fish River Subgroup contains abundant trace fossils (Geyer, 2005), including *Treptichnus pedum*, which marks the base of the type section of the Fortunian (lowermost Cambrian) at the Global Stratotype (GSSP) for the Cambrian System at Fortune Head, Canada (Narbonne et al., 1987; Brasier et al., 1994). Work by Geyer (2005) suggests that the Proterozoic–Cambrian transition in the Zaris may be located as low as the middle Schwarzrand Subgroup, however, given the absence of *Treptichnus pedum* in Schwarzrand sections within the Zaris sub-basin, we follow Grotzinger et al. (1995) in considering these sections latest Ediacaran.

3. Body fossils

This is the first report of soft-bodied Ediacaran macrobiota from the Zaris sub-basin, and expands the known geographic range of Ediacaran-type macrofossils in Namibia (see Boag et al., 2016). We recovered numerous *Aspidella*-type Billings, 1872 discoidal Ediacaran fossils both in-situ and from float material (Table 1; Figure 2). All localities preserve abundant and well-developed microbially induced sedimentary structures (‘MISS’), indicating colonization of the substrate by seafloor microbial mats.

116 In localities S.04, S.011, and S.014, *Aspidella* were discovered preserved in finer-grained
117 siltstones and shales (Table 1), at times preserving both part-and-counterpart impressions
118 (Figure 3). In localities S.015 and S.019, large *Aspidella* were found preserved in
119 negative epirelief on the top surfaces of fine-grained sandstone beds, with symmetric
120 ripples indicating influence by waves and/or bidirectional currents in relatively shallow-
121 water paleoenvironments above wave-base.

122 The affinities of *Aspidella* are controversial, however, given the consistent
123 morphological architecture and the rigid outer boundary of these forms, our reported
124 *Aspidella* fossils likely represent the rooting holdfast of frondose taxa whose affinities
125 are, at present, impossible to discern without an accompanying frond (Laflamme and
126 Narbonne, 2008). At sites S.015 and S.019, these holdfast structures are particularly
127 abundant ($n = >15$), large (up to 8 cm in diameter), and exhibit a broad size-frequency
128 distribution suggesting a well-established and tiered community at a late stage of
129 ecological succession (Figure 4). Given the robust positive relationship between
130 Ediacaran holdfast diameters and accompanying frond size (Burzynski and Narbonne,
131 2015), these *Aspidella* fossils lend themselves to analysis of population structure; we
132 therefore used Bayesian Information Criterion ('BIC'; a model-based clustering method)
133 using the package Mclust (Fraley and Raftery, 1999) in R to establish the most likely
134 number of cohorts represented in the preserved community (Darroch et al., 2013; Zamora
135 et al., 2013; Zakrevskaya, 2014; Hall et al., 2015). The results indicate virtually identical
136 BIC values for 1- and 2-group solutions when variances in groups are allowed to be
137 flexible (which is more biologically realistic than when variances are assumed equal,
138 Darroch et al., 2013). This particular assemblage may reflect a community constructed

139 through multiple recruitment events and thus composed of multiple generations. This
140 result would run counter to those from deep-water settings, but is similar to those
141 obtained from shallow-water settings where seasonal changes in temperature might be
142 expected to trigger synchronous gamete production and release (Darroch et al., 2013;
143 Zakrevskaya et al., 2014). However, since the sample size for this analysis (n=15) is
144 relatively low and we assume that these holdfasts all represent a single species, this result
145 should be considered preliminary until accompanying fronds are discovered.

146 In addition to *Aspidella*, at locality S.015 we recovered dense accumulations of
147 elongate and annulated fossils similar to those reported from the Ediacaran of China
148 preserved as positive structures on the top surfaces of beds (i.e. positive epirelief; Figure
149 2; also see Cai and Hua, 2011). These organisms are typically tube- or ribbon shaped,
150 have consistent width (1-6 mm; Figure 6), and possess closely spaced transverse
151 annulations. The tubes maintain consistent width throughout their length without conical
152 apices or evidence for flared apertures, and so are easily distinguished from other
153 precambrian tube-like organisms, such as either *Cloudina* Pflug, 1972 (which is abundant
154 throughout the Nama Group, see Grotzinger et al., 1995; Wood and Curtis, 2014), or the
155 *Cloudina*-like organism *Conotubus* (Cai et al., 2011). Even though skeletonized tubes
156 preserved in siliclastics may look similar to other soft-bodied tubes, the length of the
157 organisms described here, and presence of linked annulations (rather than cone-in-cone
158 morphology – see Hua et al., 2005) comprise strong evidence that they do not represent
159 *Cloudina*. Cohen et al. (2009) described a variety of tube-like fossils from the Nama
160 Group, including the ribbon-like taxon *Vendotaenia*, however, these are preserved
161 differently (as organic compressions), and lack the prominent annuli visible in our fossils.

The range of tube diameters fall for our organisms firmly inside the distributions recorded by Cai and Hua (2011) and Tarhan et al. (2014) for *Shaanxilithes* Xing et al., 1984, and outside those recorded for the morphologically similar (but larger) *Gaojiashania* Lin et al., 1986, allowing tentative identification as *Shaanxilithes ningqiangensis* (Figure 6e). This taxon is reported from China (Cai et al., 2012), Siberia (Zhuravlev et al., 2009), and India (Tarhan et al., 2014) where it is restricted to upper Ediacaran rocks, and has been suggested as a candidate index fossil for the latest Ediacaran (Meyer et al., 2012). In China, *Shaanxilithes* is typically preserved as two-dimensional clay molds (Meyer et al., 2012; Tarhan et al., 2014), however, the specimens reported here are instead preserved as casts and molds typical of soft-bodied Ediacaran macrofossils, in both positive and negative relief on the weathered tops and undersurfaces of fossil slabs (i.e. both positive epirelief and negative hyporelief). Individual organisms exhibit overlapping, but not crosscutting relationships, reinforcing interpretations by previous authors (Cai et al., 2011; Meyer et al., 2012) that these structures represent body fossils rather than trace fossils. Although some surface textures in association with *Shaanxilithes* could represent disarticulated individual annuli (Figure 2d), the majority are fully articulated, suggesting that the specimens were rapidly buried, or instead may have maintained a shallow infaunal (or under-mat) habit during life, and were preserved in life-position.

In addition, fossil slabs bearing dense accumulations of *Shaanxilithes* also preserve numerous *Aspidella* holdfast structures (see Laflamme et al., 2004) preserved in negative epirelief (Figure 6). Given that there is little evidence for post-mortem transport in the *Shaanxilithes* specimens (given by the low frequencies of disarticulation – see

Meyer et al., 2012), this observation would indicate that *Shaanxilithes* were likely living in extremely close association with Ediacaran frondose organisms.

4. Trace fossils

At localities S.015 and S.019, vertically oriented trace fossils (Figures 2,5) are preserved in a variety of lithologies (see Table 1) but most commonly in fine-grained and rippled sandstones indicative of shallow water, subtidal paleoenvironments. Burrows occur in the same outcrops as Ediacaran body fossils, separated by as little as ~10 cm of stratigraphy (Figure 1). In gross morphology, trace fossils are preserved as positive relief mounds on bed top surfaces (i.e. positive epirelief – Figure 2e,f,h) and as conical ‘dimples’ surrounded by concentric pits on bed bottom surfaces (i.e. negative hyporelief with positive central boss – Figure 2g). Although trace fossils often appear paired in samples (Figure 2e-h), cross-sectional views illustrate that they do not join in the subsurface as ‘u’-bends, and instead appear vertical, sometimes >5 mm in depth and typically 3-5 mm in diameter. Trace fossils truncate sedimentary laminae, which bend upwards into the burrow suggesting progressive upwards-movement of the organism in life (Figure 5b,d; Abad et al., 2006). These are best seen in thin mud drapes separating sedimentary laminae. Further evidence of upward movement of the organism during life is shown in some specimens by the preservation of stacked conical (chevron) burrow infill (‘equilibrichnion’), which represents adjustment to sediment accumulation (Desai and Saklani, 2015). The boundaries between matrix and burrow infill can be either sharp

207 or diffuse, suggesting either that mucus linings were not originally present, or that they
208 decayed before preservation in some areas.

209 The structures exhibit several features that negate an abiotic origin or
210 interpretation as water- or gas-escape structures (see e.g., Menon et al., 2016). First, the
211 conical/chevron infill visible in some examples is oriented concave-upwards, which is
212 inconsistent with gas escape (Frey et al., 2008). Moreover, no convolute bedding (which
213 is a common product of gas escape via aggregative fluidization – see Frey et al., 2008)
214 was seen in any polished sections. Although water-escape structures can sometimes result
215 in downwards-collapse of sediment (see Nichols et al., 1994; Frey et al., 2008) this
216 typically destroys structure within the column. In the structures described here, laminae
217 are more commonly seen deflected upwards into the edges of the column and preserve
218 fine-grained chevron infill (Figure 5), and are thus more consistent with the upward
219 movement of an organism. This upwards deflection of laminae into the core of the
220 burrow is particularly characteristic of some common Phanerozoic trace fossils (see e.g.,
221 Figure 5 in Abad et al., 2006), rather than gas or fluid escape. Second, in some examples
222 thin mud drapes can be seen extending laterally from the matrix down into the base of
223 infill chevrons; this illustrates that laminae are not always cross-cut (as is typical for both
224 gas- and water-escape structures), but instead sediment was able to accumulate alongside
225 the organism, and settled into the core of the burrow as the organism adjusted its position
226 upwards. Almost all of these features are at odds with the *Medusinites* and
227 *Beltanelliformis* fossils reinterpreted by Menon et al. (2016) as fluid escape structures,
228 which typically do not extend deeper than 1 mm (the examples described here penetrate
229 >5 mm), apparently rely on the presence of microbial mats for formation (which are not

evident in our examples), and do not exhibit the combination of upwards-deflected laminae and chevron cone-in-cone infill that is characteristic of biological behavior (Abad et al., 2006). Moreover, we do not see any horizontal sill-like ‘injections’ of sediment, which would suggest an abiotic origin as a sand volcano (Menon et al., 2016).

An alternative possibility is that these structures represent body fossils. A variety of putative Ediacaran trace fossils have recently been re-interpreted as body fossils belonging to elongate or tube-like epibenthic organisms (Droser et al., 2006; Droser and Gehling, 2008; Sappenfield et al., 2011), and as a result, it is possible that the structures described here represent the remains of Ediacaran soft-bodied organisms that lived anchored (or entirely) upright in the sediment. However, taphonomic experiments conducted by Menon et al. (2013) suggest that processes of gravitational sediment collapse into voids left by the decayed Ediacaran organisms do not typically produce the characteristic meniscate and ‘cone-in-cone’ infill profile seen here. Moreover, this decay-based model would also predict surface expression of collapse structures as a series of negative-relief pits (i.e. negative epirelief - Narbonne, 2005; Gehling and Narbonne, 2007); instead, our trace fossils are preserved in positive epirelief on the top-surfaces of beds.

5. Discussion

5.1 Trace fossils – The vertical trace fossils described here are best interpreted as small *Conichnus* isp. Mayannil, 1966, which belong to the family of ‘plug’ shaped burrows (Jensen and Runnegar, 2005; Buatois and Mangano, 2011). The chevron ‘cone-in-cone’

burrow infill most likely represents the activity of metazoan-grade organisms possessing radial musculature, capable of adjusting their position relative to the sediment-water interface. These burrows do bear some superficial resemblances to structures described from Ediacaran-aged sediments from the Longmynd, UK (see McIlroy et al., 2005), however, they differ from these in a number of important aspects. Although the presence of a circular depression with central mound is reminiscent of *Intrites punctatus* Fedonkin 1980 (interpreted by McIlroy, 2005 as representing lower surface of an organism that was largely sessile, but which had some propensity for movement), in cross section these structures were characterized by parallel infill penetrated less than 1 mm into the sediment; the examples described here possess unambiguous ‘cone-in-cone’ infill, and sometimes penetrate >5 mm into the sediment (indicating a much greater propensity for upwards movement, presumably in order to keep pace with sedimentation). It seems possible, however, that the *Conichnus* trace fossils reported here are part of a spectrum of movement traces (including *Intrites*) belonging to sessile, soft-bodied and gregarious metazoans that may have been relatively common in shallow marine settings in the Ediacaran.

The *Conichnus* burrows described here are relatively small compared to Phanerozoic examples; this observation matches those made by Crimes and Germs (1983), who noted unusually small sizes among a variety of Ediacaran trace fossils in Namibia (including *Bergaueria* Prantl, 1946, *Diplocraterion* Torell, 1870, and *Nereites* MacLeay in Murchison, 1839) when compared to their Paleozoic counterparts. In addition, similar burrows assigned to *Conichnus* were described by Jensen and Runnegar (2005) from the southern Witputs sub-basin known to be latest Ediacaran,

stratigraphically below sediments preserving *Pteridinium* Gürich, 1930 and the frondose taxon *Swartpuntia* Narbonne et al., 1997 (Darroch et al., 2015), confirming stratigraphic overlap between these trace fossil structures and soft-bodied Ediacara biota in southern Namibia as well. Burrows with similar morphology (albeit larger) are known from lowermost Cambrian rocks in Death Valley (Mata et al., 2012), and have a fossil record that extends throughout much of the Phanerozoic (Abad et al., 2006; Curran, 2007). Menon et al. (2013) described similar structures showing upward movement in much older Ediacaran sections from Newfoundland; however, those structures are much larger than the burrows described here, and apparently terminate in *Aspidella* holdfast-type structures usually interpreted as belonging to frondose Ediacaran organisms. We observe no direct association between *Conichnus* trace fossils and co-occurring *Aspidella*, and as such the two structures cannot be interpreted as linked.

Although it is notoriously hard to reliably match trace fossils with specific tracemakers, *Conichnus*-type burrows are almost universally attributed to anthozoan cnidarians, including sea anemones (Actinaria) and tube anemones (Ceriantharia) (Bromley, 1996; Abad et al., 2006; Buatois and Mangano, 2011; Mata et al., 2012; Menon et al., 2013; Desai and Saklani, 2015), in part through observation of living individuals in box cores (Gingras et al., 2008). Further support for inferring the existence of anthozoan cnidarians in Ediacaran ecosystems comes from divergence time estimates from molecular data, which suggest a split between Cnidaria and Bilateria in the Cryogenian, and the divergence of Medusozoa from (ancestral) anthozoans sometime in the Ediacaran (Erwin et al., 2011; Park et al., 2012). Moreover, molecular clock estimates place the origin of the Hexacorallia in the lower Cambrian, a date consistent with the

earliest known anemone body fossils (Hou et al., 2005; Rodgers, 2009). Under these circumstances it is at least plausible that anthozoans were present alongside soft-bodied Ediacara biota in the latest Ediacaran, however, in the absence of preserved body fossils to corroborate this link, this assignment must remain speculative.

5.2 The taxonomic affinity of Shaanxilithes – Despite its wide paleogeographic distribution and the abundance of material, *Shaanxilithes ningqiangensis* has been the subject of considerable taxonomic debate. More recent studies (Meyer et al., 2012; Tarhan et al., 2014) have focused on the taphonomic characteristics of this taxon, making a strong case for a body fossil, rather than trace fossil interpretation for these structures (in particular the tendency for individuals to disarticulate, producing accumulations of isolated annuli – see Meyer et al., 2012; see also Fig. 2d). Specific suggestions in terms of biological affinity have included worms, algal debris, colonial bacteria, and pogonophoran tubes (summarized in Tarhan et al., 2014). However, detailed geochemical investigation of Indian *Shaanxilithes* by Tarhan et al. (2014) using Laser-Raman spectroscopic analysis indicated that fossils were preserved as organic kerogenous compressions, comprising support for interpretation of *Shaanxilithes* as a multicellular eukaryote, and (when morphological characteristics are taken into account) a likely metazoan. Similarly, Cai et al. (2013) interpret the morphologically similar (and likely phylogenetically related) taxon *Gaojiashania* as a tube-dwelling metazoan, following detailed descriptions of complex, rigid ring-flexible bucket tube construction capable of curving, extension, and constriction.

5.3 *Mixed Ediacaran-metazoan communities* – These new fossil localities preserve Ediacaran *Aspidella*, body fossils of (probable) metazoan *Shaanxilithes*, and *Conichnus* trace fossils within 20 cm of stratigraphy. These data indicate the coexistence of two very different (and potentially of only distant phylogenetic relationship – see Xiao and Laflamme, 2009) multicellular clades, soft-bodied Ediacarans and metazoans, within latest Ediacaran ecosystems in Namibia. Although these organisms undoubtedly shared an ecosystem, the question as to whether they formed close ecological associations is more complicated and harder to test. Fossil slabs preserving dense accumulations of *Shaanxilithes* along with numerous *Aspidella* holdfasts (Figure 6) indicate that these two organisms were able to live in extremely close association, and may have exhibited more complex biotic interactions. In contrast, *Conichnus*-type burrows are not found on slabs with any evidence for any other organisms. More generally, *Conichnus* are locally abundant where they occur in sediment with ripple cross-lamination showing little evidence of colonization by microbial mats, whereas Ediacaran soft-body fossils occur in close association with MISS, but are never found on the same surfaces as *Conichnus* trace fossils. These observations are currently limited, but do suggest a preliminary model of spatial and environmental niche partitioning between Ediacaran frondose organisms and metazoan tracemakers in latest Ediacaran subtidal settings.

In a spatially heterogeneous tide- and delta-influenced shoreface environment, Ediacaran fronds and infaunal (or epibenthic) *Shaanxilithes* would have colonized mat stabilized substrates (perhaps in deeper water), with *Conichnus* trace-makers populating higher-energy and shallower sub-environments. With Ediacaran frondose organisms dependent on microbial mats for anchoring (Laflamme et al., 2011; Tarhan et al., 2010),

345 *Conichnus* trace-makers may have been able to exploit these environments relatively free
346 of competition from established Ediacaran tiered communities. In these settings, the
347 increased current velocities may have prevented cohesive mat formation (facilitating
348 anchoring and mobility in the substrate), and guaranteed a ready supply of suspended
349 organic particles and/or prey organisms.

350 This model has some support from other Ediacaran localities. Metazoan trace
351 fossils occur most frequently as isolated monospecific assemblages lacking Ediacara
352 biota (although occasionally with the infaunal and problematic taxon *Nilpenia* – Droser et
353 al., 2013) suggesting that niche partitioning between these two organismal groups
354 extends back at least until the mid-Ediacaran. Typical exclusivity between Ediacara biota
355 and metazoan trace fossils is supported both in older sections from Mistaken Point in
356 Newfoundland, Canada (Liu et al., 2010; 2014), and in late Ediacaran trace fossil
357 assemblages lacking Ediacaran macrofossils altogether (Pecoits et al., 2012). Some rare
358 exceptions to this rule are known, including the probable mollusk *Kimberella*, which is
359 often found within diverse communities of more enigmatic Ediacaran organisms, or the
360 lowermost Cambrian association between Erniettomorph-like fronds and complex trace
361 fossils (including *Treptichnus pedom*) described by Jensen et al. (1998) from south
362 Australia. This may indicate that direct interactions between Ediacaran- and Cambrian-
363 type organisms only really became common following the Ediacaran-Cambrian
364 transition, when it may have been forced by the rapid diversification of animal groups
365 and expansion into new ecospace.

366

5.4 *Latest Ediacaran communities and the ‘biotic replacement’ model* – The biotic replacement model for the Ediacaran-Cambrian transition suggests that early members (or precursors) of the Cambrian evolutionary fauna gradually displaced Ediacaran biotas through a combination of predatory displacement and ecological engineering of Ediacaran-type ecosystems (Laflamme et al., 2013; Darroch et al., 2015; Schiffbauer et al., in press; see also Seilacher, 1992; Bengtson and Yue, 1992; Hua et al., 2003). These new fossil localities support the inference of both stratigraphic and ecological overlap between these two organismal groups, and so fulfills a fundamental prediction of the model. However, evidence for direct biotic interactions between soft-bodied Ediacara biota and Cambrian-style metazoans (and thus providing concrete mechanisms for ‘biotic replacement’) is still sparse. For example, there is no evidence as yet for predation on soft-bodied Ediacaran organisms. The high frequency of drill holes in *Cloudina* from latest Ediacaran reefs (Hua et al., 2003) certainly indicates that metazoan predation had emerged as an ecological strategy for nutrient acquisition, however, *Cloudina* (and other biomineralizing taxa such as *Namacalathus*) are more commonly thought of as metazoans (Wood and Curtis, 2015; Wood et al., 2015; Schiffbauer et al., in press). As such, evidence for wide-spread predatory activities on soft-bodied sessile Ediacarans is still lacking. Interpretation of *Conichnus* burrows as being produced by anthozoan cnidarians (e.g., Frey and Howard, 1981; Bromley, 1996; Abad et al., 2006; Buatois et al., 2014; Desai and Saklani, 2015) does offer a possible mechanism - all anthozoans are predatory (using nematocyst stinging cells), and most likely evolved as predators adapted to catching and digesting relatively large prey items via either filter feeding or passive predation (Hand, 1963). In the event that representatives of the Ediacara biota possessed

a mobile larval or dispersal stage early in development (Clapham et al., 2003; Darroch et al., 2013; Wood and Curtis, 2014), it is conceivable that these may have been prey for emerging Cambrian-type predatory and/or filter-feeding animals. However, in the absence of anthozoan body fossils the *Conichnus* trace fossil-trace maker link remains unproven, and a model of Ediacaran passive predation by anthozoans must be viewed as speculative.

The evidence for increasing ecosystem engineering in the latest Ediacaran is more compelling. Although ‘ecosystem engineering’ refers to a variety of trophic and non-trophic biological processes (Erwin and Tweedt, 2011), it is most commonly preserved in the rock record as trace fossils showing vertical disruption of the sediment column and sediment-water interface. Recent work in the Nama Group has uncovered a suite of trace fossils with far higher diversity than any of those recorded for older Ediacaran settings, including *Conichnus*, *Strepichnus narbonnei*, *Olenichnus* (Jensen and Runnegar, 2005), *Nereites* (Bouougri et al., 2007), and a horizontal feeding burrow resembling *Zoophycus* (Mcdonald et al., 2014). These discoveries provide clear evidence for an increasing diversity and intensity of metazoan activity, which likely had a profound effect on Ediacaran ecosystems (Laflamme et al., 2013; Erwin and Valentine, 2013). Impacts likely included (but were not limited to) changes in the oxygenation state of the oceans, the distribution of nutrients in the water column, and the stability of benthic substrates (Erwin and Tweedt, 2011). This inference matches well with the appearance of metazoan and filter-feeding reef builders, which show evidence for episodes of pulsed recruitment and philopatric larval aggregation (Wood and Curtis, 2014). Taken together, these lines of evidence illustrate a pronounced change in the character and volume of suspended

particulate organic matter (and potentially zooplankton – see Butterfield, 2009) from earlier in the Ediacaran, and suggest an oceanic ecosystem that differs dramatically from the older Ediacaran successions preserved in South Australia and Russia.

Conclusions

The new fossil localities described here extend the known geographic range of soft-bodied Ediacara biota to include the Zaris sub-basin of southern Namibia. The co-occurrence of soft-bodied Ediacara biota and metazoan trace fossils supports inference of unusual latest Ediacaran shallow-water ecosystems comprising two very different branches of eukaryotic life. Although the precise nature of biotic interactions between Ediacarans and metazoans is still unclear, these new localities indicate stratigraphic and ecological overlap between these two organismal groups, and so fulfills a fundamental prediction of the biotic replacement model. Preliminary observations of a mutual exclusivity between frondose Ediacara biota and metazoan trace fossils in these new localities may suggest a form of niche partitioning, and thus inference of limited direct biotic interactions between these two organismal groups. Although the data supporting this are currently limited, and we cannot as yet test the significance of these associations with any statistical power, they do help form a hypothesis that can be tested with future fossil discoveries.

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Figure and table captions

Figure 1 – Locality figure, illustrating: a) the distribution of Nama Group sediments in
southwest Africa. b) The distribution of new fossil sites along the D850 and D855 roads,
in the vicinity of Zebra River Farm. c) Generalized stratigraphy of the Zaris sub-basin in
the vicinity of Zebra River, and approximate position of fossil sites described in this
study; section logs are given for the two sites where both *Aspidella* fossils and *Conichnus*

653 burrows were recovered in-situ. Base map in a) and regional log section in c) redrawn
654 from Grotzinger et al. (2000).

655
656 Figure 2 – Ediacara biota and trace fossils recovered from new fossil sites in the
657 Schwarzsand subgroup: a-b) *Aspidella*; c-d) *Shaanxilithes* cf. *ninqiangensis* preserved in
658 three dimensions; e-i) *Conichnus* sp. trace fossils preserved on collected slabs. Note that
659 e, f, and h illustrate preservation in positive epirelief on slab topsurfaces, while g
660 illustrates ‘dimple’ shaped morphology on bottom surfaces (negative hyporelief with
661 positive hyporelief in center). Filled scale bars 1 cm; open scale bars 1 mm.

662
663 Figure 3 – Exceptional part and counterpart preservation in *Aspidella* collected from
664 locality S.04. Also note presence of MISS on same slab. Scale bars in cm.

665
666 Figure 4 – Large *Aspidella* (negative epirelief) collected from locality S.015. Highlighted
667 areas show examples of (b) radiating and ‘tentaculate’ structures present around several
668 of the holdfasts, and (c) variable morphology of holdfast ‘plugs’, suggesting preservation
669 in a variety of localized taphonomic styles. Holdfast size-frequency (diameter, n=15) and
670 cluster analysis plots are shown in d); wide range of holdfast sizes suggests a mature
671 stand of frondose Ediacaran taxa in a late stage of ecological succession. Size frequency
672 plot suggests a bimodal distribution of holdfast sizes, likely representing two separate age
673 classes (cohorts) in the frond population. Scale bars represent 1 cm increments.

Figure 5 – Polished sections through *Conichnus* traces illustrating internal features: a) two closely associated vertical burrows (arrowed) clearly cutting through laminae ('Tr'), and showing gross morphology with domed topsurfaces (positive epirelief, 'Do') and 'dimple'-shaped morphologies ('Di') on the bottom surfaces (hyporelief). Note that burrows do not show any tendency to join as a 'u-bend'. b) and c) show enlarged views of the same traces, illustrating both sharp (white arrow) and diffuse (black arrow) interfaces between matrix and burrow fill. The differences between more homogenous sediment (although preserving faint traces of cone-in-cone structure) inside burrows ('Hs') and undisrupted/laminated sediment in matrix ('Ls') are also clear. d) and e) show two different burrows possessing the same characteristics as those figured in a-c), note shallow meniscate (cone-in-cone) infill to burrows and thin mud drapes ('Md') that deflect up into burrow margins, indicating upwards movement of the tracemaker during life. Scale bars 1 mm.

Figure 6 – *Shaanxilithes* cf. *ningqiangensis* from locality S.015, with tube diameter measurements and comparison (e) with the morphologically similar taxon *Gaojiashania* (diameter range data from Cai et al., 2011). White arrows indicate in-place holdfast structures, illustrating that *Shaanxilithes* lived in close association with frondose Ediacaran taxa. Black arrows indicate instances of tight coiling, suggesting that tubes were likely flexible in life. Black arrow with white border in d indicates an example of where discs have 'slipped', possibly post-mortem and after degradation of tube walls. Scale bars represent 1 cm increments.

698 Table 1 – Details of collected fossil material, lithology and presence/absence of trace
699 fossils for new fossil localities from the Schwarzrand Subgroup, southern Namibia (see
700 also Fig. 1). All collected specimens are accessioned in the Geological Survey of
701 Namibia, Windhoek.

Table 1

1

Site ID	Fossils	Sample no.	Lithology & sedimentology	Notes
S.01	Erniettomorph	S.01(1)	Thin-bedded siltstones and shales w. occ. rippled horizons	Abundant MISS on loose slabs; also rare flute casts
S.04	Aspidella	S.04(1)	Thin-bedded siltstones and shales w. occ. rippled horizons	Trio of Aspidella preserved w. MISS
S.011	Aspidella	S.011(1-2)	Laminated siltstones and shales	Abundant MISS
S.014	Aspidella	S.014(1)	Thin-bedded siltstones w. occ. rippled horizons	In-situ outcrop
S.015	Shaanxilithes; Aspidella (Hiemalora?) Bergaueria	S.015(5-12)	Slabby siltstones and fine-grained sandstones; thicker sstn. beds (5-10 cm thick) w. rippled topsurfaces – see Fig. 1	Conichnus sp. common on slab topsurfaces
S.018	Aspidella	NA	Siltstones w. occ. rippled horizons	In-situ outcrop
S.019	Aspidella	NA	Siltstones and fine sandstones; thicker sstn. beds w. rippled topsurfaces – see Fig. 1	Riverbed section w. in-situ outcrop & Conichnus - see Fig. 1

2

3 Table 1

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6