



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



Simon A.F. Darroch^{a,b,*}, Thomas H. Boag^c, Rachel A. Racicot^{b,d}, Sarah Tweedt^b, Sara J. Mason^e, Douglas H. Erwin^b, Marc Laflamme^e

^a Department of Earth and Environmental Sciences, Vanderbilt University, 2301 Vanderbilt Place, Nashville, TN 37235-1805, USA

^b Smithsonian Institution, PO Box 37012, MRC 121, Washington, DC 20013-7012, USA

^c Department of Geological Sciences, Stanford University, 450 Serra Mall, Building 320, Room 118, Stanford, CA 94305-2115, USA

^d The Dinosaur Institute, Natural History Museum of Los Angeles County, 900 Exposition Blv., Los Angeles, CA 90007, USA

^e Department of Chemical and Physical Sciences, University of Toronto Mississauga, 3356 Mississauga Road North, Ontario L5L 1C6, Canada

ARTICLE INFO

Article history:

Received 2 April 2016

Received in revised form 26 June 2016

Accepted 2 July 2016

Available online 4 July 2016

Keywords:

Ediacaran

Cambrian

Metazoans

Trace fossil

Ecosystem engineering

Conichnus

Shaanxilithes

Aspidella

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.

© 2016 Elsevier B.V. All rights reserved.

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 Jensen et al., 2005; 2006; Sappinfield et al. 2011), such that *Helminthoidichnites* is the only trace fossil from this interval still universally viewed as

* Corresponding author at: Department of Earth and Environmental Sciences, Vanderbilt University, 2301 Vanderbilt Place, Nashville, TN 37235-1805, USA.

E-mail addresses: simon.a.darroch@vanderbilt.edu (S.A.F. Darroch), tomboag@stanford.edu (T.H. Boag), rracicot@nhm.org (R.A. Racicot), tweedt@si.edu (S. Tweedt), s.mason@mail.utoronto.ca (S.J. Mason), Erwind@si.edu (D.H. Erwin), marc.laflamme@utoronto.ca (M. Laflamme).

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 (Fig. 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; Fig. 2). All localities preserve abundant and well-developed microbially induced sedimentary structures ('MISS'), indicating colonization of the substrate by seafloor microbial mats. In localities S.04, S.011, and S.014, *Aspidella* were discovered preserved in finer-grained siltstones and shales (Table 1), at times preserving both part-and-counterpart impressions (Fig. 3). In localities S.015 and S.019, large *Aspidella* were found preserved in negative epirelief on the top surfaces of fine-grained sandstone beds, with symmetric ripples indicating influence by waves and/or bidirectional currents in relatively shallow-water paleoenvironments above wave-base.

The affinities of *Aspidella* are controversial, however, given the consistent morphological architecture and the rigid outer boundary of these forms, our reported *Aspidella* fossils likely represent the rooting holdfast of frondose taxa whose affinities are, at present, impossible to discern without an accompanying frond (Laflamme and Narbonne 2008). At sites S.015 and S.019, these holdfast structures are particularly abundant ($n \geq 15$), large (up to 8 cm in diameter), and exhibit a broad size-frequency distribution suggesting a well-established and tiered community at a late stage of ecological succession (Fig. 4). Given the robust positive relationship between Ediacaran holdfast diameters and

accompanying frond size (Burzynski and Narbonne 2015), these *Aspidella* fossils lend themselves to analysis of population structure; we therefore used Bayesian Information Criterion ('BIC'; a model-based clustering method) using the package Mclust (Fraley and Raftery, 1999) in R to establish the most likely number of cohorts represented in the preserved community (Darroch et al. 2013; Zamora et al., 2013; Zakrevskaya, 2014; Hall et al., 2015). The results indicate virtually identical BIC values for 1- and 2-group solutions when variances in groups are allowed to be flexible (which is more biologically realistic than when variances are assumed equal, Darroch et al. 2013). This particular assemblage may reflect a community constructed through multiple recruitment events and thus composed of multiple generations. This result would run counter to those from deep-water settings, but is similar to those obtained from shallow-water settings where seasonal changes in temperature might be expected to trigger synchronous gamete production and release (Darroch et al. 2013; Zakrevskaya et al., 2014). However, since the sample size for this analysis ($n = 15$) is relatively low and we assume that these holdfasts all represent a single species, this result should be considered preliminary until accompanying fronds are discovered.

In addition to *Aspidella*, at locality S.015 we recovered dense accumulations of elongate and annulated fossils similar to those reported from the Ediacaran of China preserved as positive structures on the top surfaces of beds (i.e. positive epirelief; Fig. 2; also see Cai and Hua 2011). These organisms are typically tube- or ribbon shaped, have consistent width (1–6 mm; Fig. 6), and possess closely spaced transverse annulations. The tubes maintain consistent width throughout their length without conical apices or evidence for flared apertures, and so are easily distinguished from other precambrian tube-like organisms, such as either *Cloudina* Pflug 1972 (which is abundant throughout the Nama Group, see Grotzinger et al. 1995; Wood and Curtis 2014), or the *Cloudina*-like organism *Conotubus* (Cai et al. 2011). Even though skeletonized tubes preserved in siliciclastics may look similar to other soft-bodied tubes, the length of the organisms described here, and presence of linked annulations (rather than cone-in-cone morphology – see Hua et al. 2005) comprise strong evidence that they do not represent *Cloudina*. Cohen et al. (2009) described a variety of tube-like fossils from the Nama Group, including the ribbon-like taxon *Vendotaenia*, however, these are preserved 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* (Fig. 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 (Fig. 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 (Fig. 6). Given that there is little evidence for post-mortem transport in the *Shaanxilithes* specimens

Download English Version:

<https://daneshyari.com/en/article/4465632>

Download Persian Version:

<https://daneshyari.com/article/4465632>

[Daneshyari.com](https://daneshyari.com)