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Biological and Ecological Insights from the Preservational Variability of *Funisia dorothea*, Ediacara Member, South Australia

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by

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ABSTRACT OF THE THESIS

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The Ediacara Biota represent a turning point in the evolution of life on Earth, signifying the transition from single celled organisms to complex, community-forming macrobiota. The exceptional fossil record of the soft-bodied Ediacara Biota provides critical insight into the nature of this transition and into ecosystem dynamics leading up to the so-called "Cambrian Explosion." However, the preservation of non-biomineralizing organisms in a diversity of lithologies goes hand-in-hand with considerable taphonomic complexity that often shrouds true ecological and biological signatures. We address the nature of this taphonomic complexity within the fossiliferous sandstones of the Ediacara Member in South Australia. Utilizing the most data-rich and well-preserved outcropping of the Ediacara Member, the Nilpena Station National Heritage Ediacara Fossil Site, we conduct a focused, taxon-level taphonomic characterization of the tubular organism *Funisia dorothea. Funisia* is the most abundant

body fossil in the Ediacara Member, making its taphonomic characterization essential to the accurate interpretation of regional paleobiology and paleoecology. We identify two primary modes of *Funisia* population structure, cluster-type and surface-type packages, each of which exhibit distinct suites of taphonomic variation in individual *Funisia*. Within the two package types, four preservational modes of *Funisia* are identified: convex external molds, concave external molds, convex internal molds, and concave internal molds. Among macrofossils at Nilpena, this tiered preservational complexity is unique to *Funisia*; its systematic classification elucidates population-level biostratinomy at Nilpena as well as aspects of *Funisia's* paleobiology and autecology.

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INTRODUCTION

The Ediacara Biota occupy a uniquely significant place in Earth's history as the first complex macroscopic organisms (599-541 Ma) (Boag et al. 2016), spanning the gap between the microbially-dominated ecosystems of the mid-Proterozoic and the rise of metazoan-dominated ecosystems in the Cambrian. While investigations of morphology and ontogeny have broadly constrained the phylogenetic placement of several Ediacara organisms (e.g., *Kimberella* as a potential stem-mollusk; *Dickinsonia* as a stem-metazoan) (Fedonkin and Waggoner 2003; Droser and Gehling 2015; Evans et al. 2017), many of their characters, including their biology, ecology, and evolutionary significance, remain unclear. While commonly accredited to the "alien" appearance of the Ediacara Biota (Lewin 1984), the enigmatic nature of late Neoproterozoic communities is, to some extent, a consequence of the paucity of systematic taphonomic investigation at the taxon scale. Taxon-focused taphonomic studies allow for the identification of thus far unacknowledged taxon-specific taphonomic biases which may obfuscate recognition of true taxonomic diversity and community-level structure, as well as veil the biostratinomic and diagenetic processes responsible for Ediacara fossilization (Tarhan et al. 2015).

Historically, Ediacaran paleontology has been hindered by an oversight of taphonomic complexity, with the majority of initial investigations being premised on the characterization of individual museum samples, a methodology that fails to contextualize fossils within a broader taphonomic, paleoenvironmental, and paleoecological context. A growing number of studies, however, have begun to demonstrate the utility of taphonomic contextualization in investigations of the paleoecology and affinities of

Ediacaran organisms. This has resulted in the recognition of several critical aspects of these assemblages, such as intra-taxon taphomorphic variability (Tarhan et al. 2010; Liu et al. 2015), reproductive strategies (Droser and Gehling 2008; Hall et al. 2015; Mitchell et al. 2015), mobility (Evans et al. 2019a), constraints on biomaterials (Evans et al. 2019b), and recognition of the dominance of tubular taxa (Jensen et al. 2006; Droser and Gehling 2008; Cohen et al. 2009; Sappenfield et al. 2011; Joel et al. 2014; Tarhan et al. 2018).

Pertinent to this study is the re-envisioning of the Ediacara Biota as a tube-dominated assemblage (Jensen et al. 2006; Schiffbauer et al. 2016) through a critical review of the Precambrian trace fossil record from a taphonomic perspective (e.g., Jensen et al. 2006). This new approach to interpreting Precambrian trace fossils from a preservational perspective led to the recognition that many purported bilaterian-created trace fossils are better interpreted as body fossils of tubular organisms, largely on the grounds that tubular body fossils often preserve wrinkle structures and do not present characters typical of trace fossils such as displaced sediment and consistent width. These tubular taxa, defined by their elongate, simple, and hollow body forms, are now known to out-number all other morphotypic groups within the Ediacara Member by an order of magnitude and are highly abundant in globally distributed Ediacara strata.

While they are now generally accepted to be the most abundant and ecologically diverse morphotype in the Neoproterozoic (Gehling and Droser 2009; Schiffbauer et al. 2016), a taphonomic framework for tubular taxa−under which the development of taxonomic distinctions and paleoecological associations can be made−remains

incomplete. Therefore, knowledge of this globally significant grouping remains incomplete and is further obscured through the unusual taphonomic complexity often observed in tubes, due to their elongate and hollow body structures (Wade 1968; Gehling 1999; Droser and Gehling 2008). The taphonomic complexity corresponding to the tubular morphotype has, thus far, precluded the detection of whether morphotypic similarities among tubular taxa reflect homology or convergence. Herein, through the systematic taphonomic description of the most abundant tubular organism preserved in the Ediacara Member of South Australia, *Funisia dorothea* (Droser and Gehling 2008), we provide a basis for defining the unique preservational complexity of tubular taxa. *Funisia* preservation is particularly notable because its taphonomic complexity is confounded by the characteristic dense packing of *Funisia* individuals, resulting in fossiliferous surfaces covered by overlapping *Funisia* in various preservational modes and states of character degradation. Utilizing the large dataset available at the Nilpena Station National Heritage Ediacara Fossil Site in South Australia, *Funisia's* complexity is defined through a systematic, taphonomically-focused approach in order to clarify aspects of *Funisia* paleoecology and paleobiology, as well its impact on community-level biostratinomy.

GEOLOGIC SETTING AND METHODS

The Ediacara Member of the Rawnsley Quartzite is exposed within and west of the Flinders Ranges in South Australia, the most extensively documented fossiliferous outcropping of which is exposed at the Nilpena Station National Heritage Ediacara Fossil

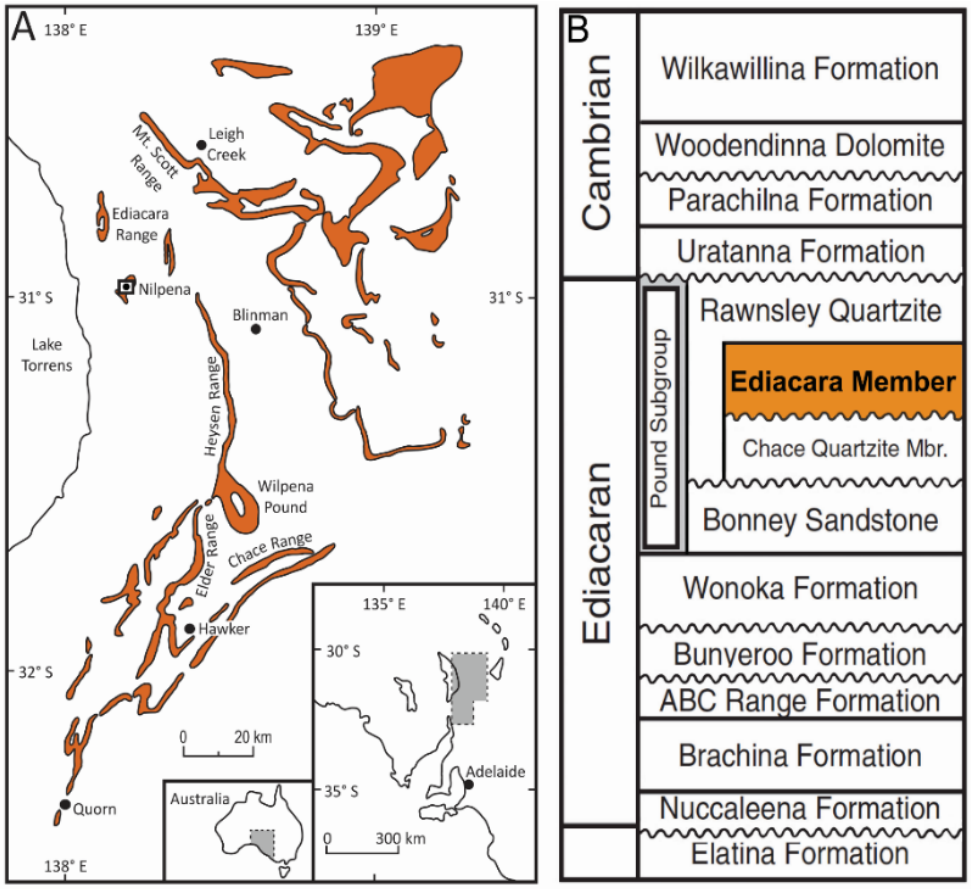


FIGURE 1—Geologic context of the fossiliferous Ediacara Member of South Australia. **A**) Locality information. Ediacara Member in orange, the Nilpena Station National Heritage Ediacara Fossil Site is denoted by a white box. **B**) Stratigraphic cross section. Relative location of the Ediacara Member is highlighted. Modified from Gehling 2000.

Site (Fig. 1). Located 200–600 m below a basal Cambrian disconformity, the Ediacara Member hosts a diversity of Ediacara fossils that, given their similarity to broadly contemporaneous fossil assemblages of Russia are considered part of the White Sea Assemblage (Gehling 2000; Droser et al. 2006).

Representing deposition across a range of shallow marine and deltaic settings, the Ediacara Member is characterized by four fossiliferous facies: Flat-Laminated to Linguoid-Rippled Sandstone, Channelized Sandstone and Sand Breccia, Oscillation-

Rippled Sandstone (ORS), and Planar Laminated and Rip-up Sandstone (PLRUS) (Gehling and Droser 2013; Droser et al. 2017; Tarhan et al. 2017). Each facies is associated with a distinct assemblage of Ediacara body fossils, traces, and textured organic surfaces (Gehling and Droser 2009, 2013; Tarhan et al. 2017).

Of the four facies comprising the Ediacara Member, *Funisia* is found primarily in the ORS and the PLRUS facies where it occurs in similar abundances (Gehling and Droser 2009). The ORS facies is characterized by thinly bedded, rippled fine- to coarse-grained feldspathic quartzarenite, and records deposition between fair-weather and storm wave base (Gehling and Droser 2013; Tarhan et al. 2017). The PLRUS facies is characterized by laterally continuous, planar-laminated fine-grained quartzarenite beds, representing an upper sub-wave base canyon-fill deposit (Gehling and Droser 2013; Tarhan et al. 2017). Bedding planes in both facies exhibit similar lithologies and small variations in grain size; differential preservation is therefore less likely to be attributable simply to the textural properties of the burial sand body and is more likely due to variation in the sedimentological and biostratinomic processes responsible for the death and burial of *Funisia* communities.

The Ediacara Member is well-known for exceptional preservation of the soft-bodied Ediacara Biota as instantaneous "snapshot" deposits, reflecting the rapid burial of *in situ*, living communities by storm events. Episodic obrution of these communities resulted in the molding and casting of organisms on the sole surfaces of successive bedding planes, which persist through diagenesis as discrete bedforms, even in the absence of textural disparities between adjacent beds. This anactualistic non-

amalgamation of adjacent, lithologically similar bedforms, that cast instead of erode underlying ripples, is attributed to the ubiquitous presence of organic biofilms and matgrounds, coupled with early-initiating precipitation of authigenic cements (Tarhan et al. 2016, 2017). As a result of these processes, assemblages of soft-bodied organisms are preserved in exceptional detail on the bases of discrete, successive bedding planes within the Ediacara Member. Mode of preservation (e.g., concave or convex hyporelief) is largely taxon-dependent (Wade 1968; Gehling 1999); taxa preserved as concave hyporelief external molds (e.g., *Dickinsonia*) are inferred to have been composed of material resistant to collapse upon burial, whereas fossils preserved as convex hyporelief external or internal molds (e.g., *Aspidella*) are inferred to represent organisms that collapsed or were infilled upon burial, respectively (Gehling 1999; Gehling 2000; Evans et al. 2015).

The unamalgamated nature of bedform packages in the Ediacara Member allows for the excavation and reconstruction of entire bedding planes at Nilpena, where successive layers of sandstone are excavated from an outcrop, flipped to reveal the fossiliferous bedding sole, and reassembled to reconstruct discrete pieces, of up to 25 m^2, of fossilized Ediacara seafloor (Droser et al. 2019). A total of 38 discrete fossiliferous bedding planes have been excavated and reconstructed at Nilpena, exposing over 300 m^2 of fossiliferous surface and providing a large, diverse dataset of Ediacara organisms preserved within an ecological context through time and space (Droser et al. 2019).

Funisia specimens discussed herein are located at the Nilpena National Heritage Ediacara Fossil Site as well as within the collections of the South Australian Museum in

Adelaide. Observations at Nilpena recognized five reconstructed bedding planes and two discrete, but unassembled, bedforms in the ORS and PLRUS facies on which *Funisia* is the dominant taxon (Table 1). On these bedding planes *Funisia* occur either covering the entire surface of multiple square meters (surface-type assemblages) or as multiple discrete stands (< 0.5 m^2 each) of *Funisia* distributed across the bedding plane (cluster-type assemblages) (Fig. 2). Total *Funisia* abundance counts are complicated by the nearly ubiquitous occurrence of densely packed and overlapped individuals covering entire fossiliferous surfaces of up to 10 m^2. Only two of the seven *Funisia*-dominated

TABLE 1.—*Funisia*-dominated bedding plane details and abundance estimates.

	Bed	**Facies**	**Area** (m^2)	***Funisia* estimate** (per m^2)	**Total *Funisia* population**
Surface-type	TC-MM2	ORS	10.3	3,925 – 4,525	40,428 –46,612
	STC-Maw *	ORS	2.3	911 – 2,100	2,095 –4,830
	STC-X	ORS	9.0	2,425 –5,050	21,825 – 45,450
	WS-MAB	PLRUS	3.3	3,300 – 6,433	10,890 – 21,229
	WS-JDB *	PLRUS	7.5	2,500 – 6,100	18,750 – 45,750
Cluster-type	TB-BRW	ORS	9.3	N/A	421 **
	LV-FUN	PLRUS	10	N/A	483 **

* = Not an assembled bed
** = Reported value is a direct count, not an estimate

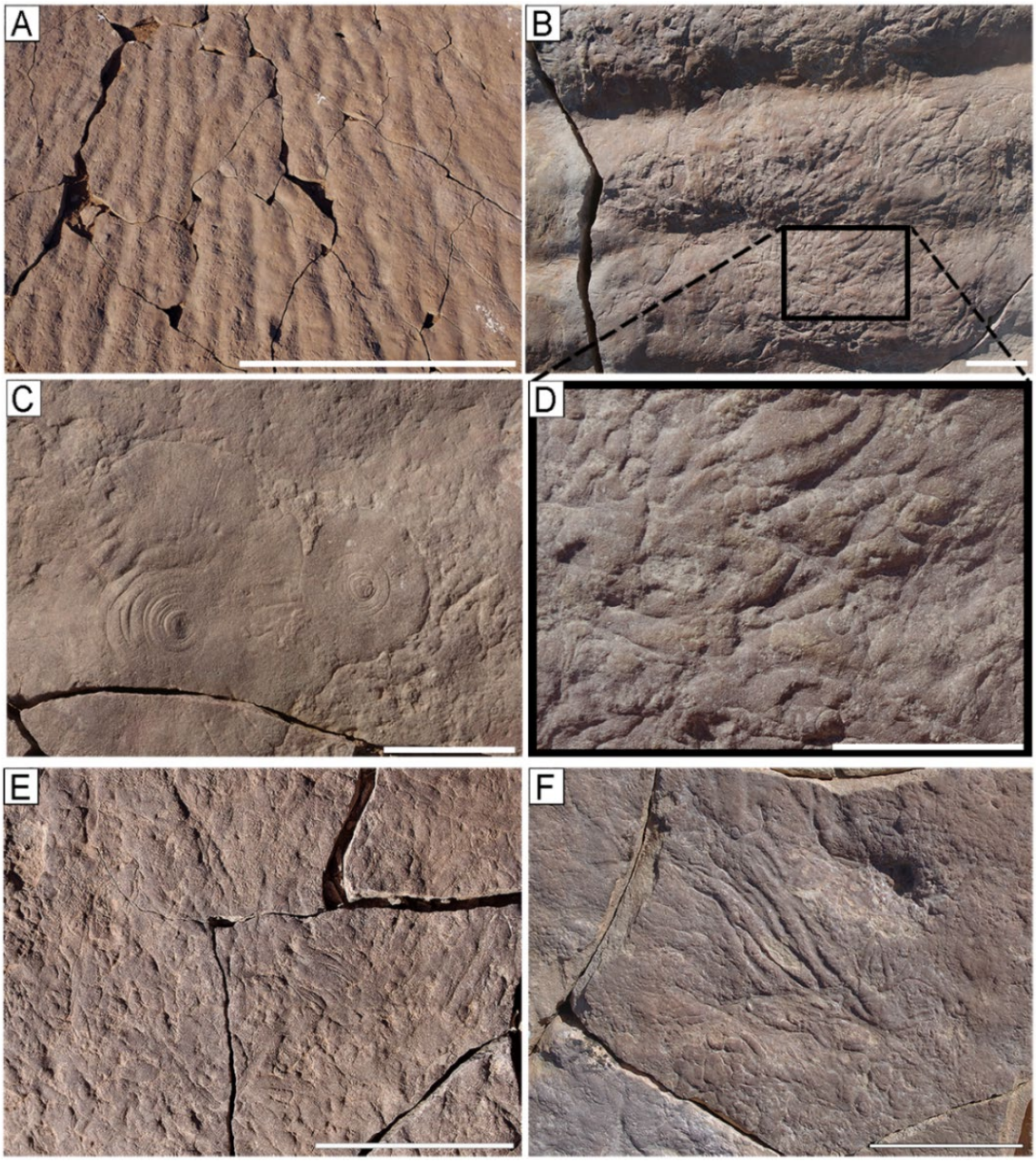


FIGURE 2 —Examples of surface-type and cluster-type *Funisia dorothea* populations. **A**) Bedding plane TC-MM2 exhibiting surface-type *Funisia* covering the entire photographed surface (~1.5 m^2); scale=1 m. **B**) Cluster-type *Funisia* on TB-BRW; scale=5 cm. **C**) Surface-type *Funisia* on TC-MM2, note low detail *Funisia* wrapping around high detail *Aspidella*; scale=5 cm. **D**) Cluster-type *Funisia* on TB-BRW; from black box in B; scale=5 cm. **E**) Surface-type *Funisia* on WS-MAB; scale=5 cm. **F**) Cluster-type *Funisia* on LV-FUN, note juxtaposition of central cluster with a distinct non-*Funisia* textured organic surface; scale=5 cm.

beds at Nilpena preserve cluster-type *Funisia* with relatively low amounts of body fossil overlap, thus lending themselves to accurate individual counts (Table 1). The remaining five beds preserve such highly overlapped and poorly preserved *Funisia* populations that accurate counts are impossible, thus necessitating population estimates.

On each of these *Funisia* surfaces, a series of three counts within 10 x 10 cm quadrats were carried out. In each quadrat, *Funisia* individuals were traced to their visible extent and where the continuity of an individual was questionable, were counted in two ways. In the first we erred towards assuming two individuals, acknowledging that the resulting number of individual tubes was likely underestimated. In the second approach we counted potentially continuous tubes as one individual, resulting in the possible underestimation of *Funisia* abundance. Quadrat estimates were then extrapolated to the full area covered by the *Funisia* package (i.e., bedding plane area) to give an area-standardized upper and lower estimate of population size as is reported in Table 1.

In earlier publications (i.e., Droser and Gehling 2008), bed-scale *Funisia* populations were proposed to represent size-similar cohorts, suggestive of sexual reproduction via spatfall. We test this hypothesis using only the most taphonomically robust forms of *Funisia* for the construction of population size distributions. Unimodality of the resulting distributions was tested for using the Hartigan Dip test statistic for unimodality/multimodality, a commonly utilized test for interpreting distribution modality wherein the null hypothesis assumes unimodality (Hartigan and Hartigan 1985).

Defining Taphonomic Variability

Funisia represents a taphonomically unique member of the Ediacara Biota at Nilpena attributable both to its abundance and its preservation in four distinct manners. Instead of being defined by one mode of preservation as are the majority of the Ediacara macrobiota (e.g., all *Dickinsonia* body fossils are preserved as concave external molds), *Funisia* is characterized by four distinct modes of preservation: convex or concave external molds and convex or concave internal molds (Fig. 3).

For the remainder of this discussion concave and convex forms will be referred to as negative relief and positive relief molds, respectively, reflecting the fossil's relief on the base of reconstructed bedding planes. Additionally, *Funisia* are found to possess

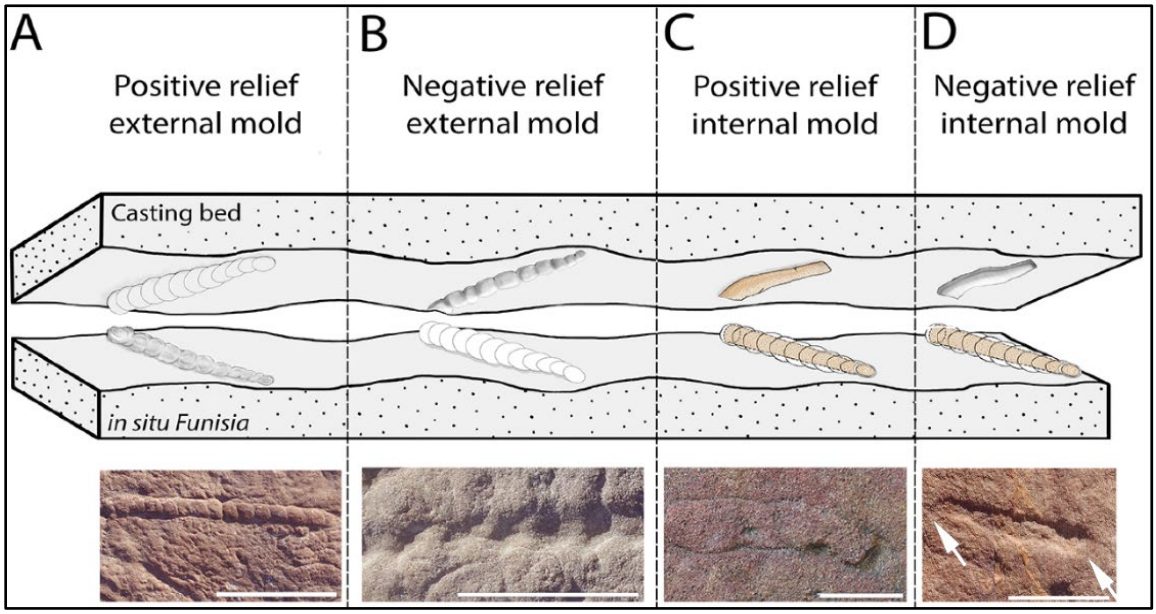


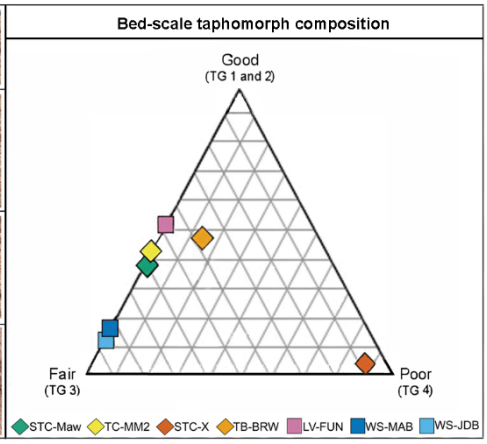
FIGURE 3—Schematic of *Funisia dorothea* preservational modes. Illustrations show the casting bed (top) and the seafloor with *in situ Funisia* (bottom). Photographs provide examples of each preservational mode from bedding planes at Nilpena. **A**) Positive relief external mold, scale = 3 cm. **B**) Negative relief external mold, scale = 3 cm. **C**) Positive relief internal mold, SAM P40725, scale = 2 cm. **D**) Negative relief internal mold, arrows indicating sub-parallel terminations; scale = 3 cm.

multiple modes of preservation within individual tubes (referred to as multi-part preservation), exhibiting transitions between positive and negative external molds or from external molds to internal molds within a single tube (Fig. 4). This supports the interpretation of isolated internal molds as *Funisia* fossils despite a lack of diagnostic features such as modularity and scalloped margins (Fig. 3C, D).

In addition to a variety of preservational modes, *Funisia* also exhibit a range of taphonomic grades within positive relief externally molded specimens, representing the only *Funisia* taphomorph that exhibits variability in the integrity of external features between individuals. The identification of biostratinomic factors contributing to this added complexity requires further description of the various degradation states observed. We define these degradation states as taphonomic grades on an ordinal scale (TG 1-4)

TABLE 2.—Variation in module definition in positive relief external molds of *Funisia dorothea* in relationship to assigned taphonomic grade and preservational integrity. Taphonomic grade refers to the placement of the four *Funisia* taphomorphs on an ordinal scale with corresponding preservation classifications. All scales = 2 cm. Ternary taphogram plots bedding planes by the relative abundances of taphonomic grade classifications; PLRUS facies associations represented by squares, ORS facies associations represented by diamonds. Ternary plotting sheet from Marshall, 1996.

Taphonomic Grade	Classification	Distinguishing Features	
1	Good	• Serial units preserved • Scalloped lateral margins • Sharp margins	
2	Good	• Serial units rarely preserved • Scalloped lateral margins • Variable sharpness along lateral margins	
3	Fair	• Serial units not preserved • Lateral margins are parallel lines, no scalloping • Poorly defined margins • Tube overlap is common	
4	Poor	• Tapered terminations • Rare lateral association with better preserved *Funisia* (TG 2-3)	



(Table 2) based on the presence of features that are characteristic of the best-preserved *Funisia* (e.g., modularity, Droser and Gehling, 2008). All identifiable positive relief external molds preserved on the seven *Funisia*-dominated bedding planes at Nilpena were assigned taphonomic grade values and were further described by their short-axis widths and orientations.

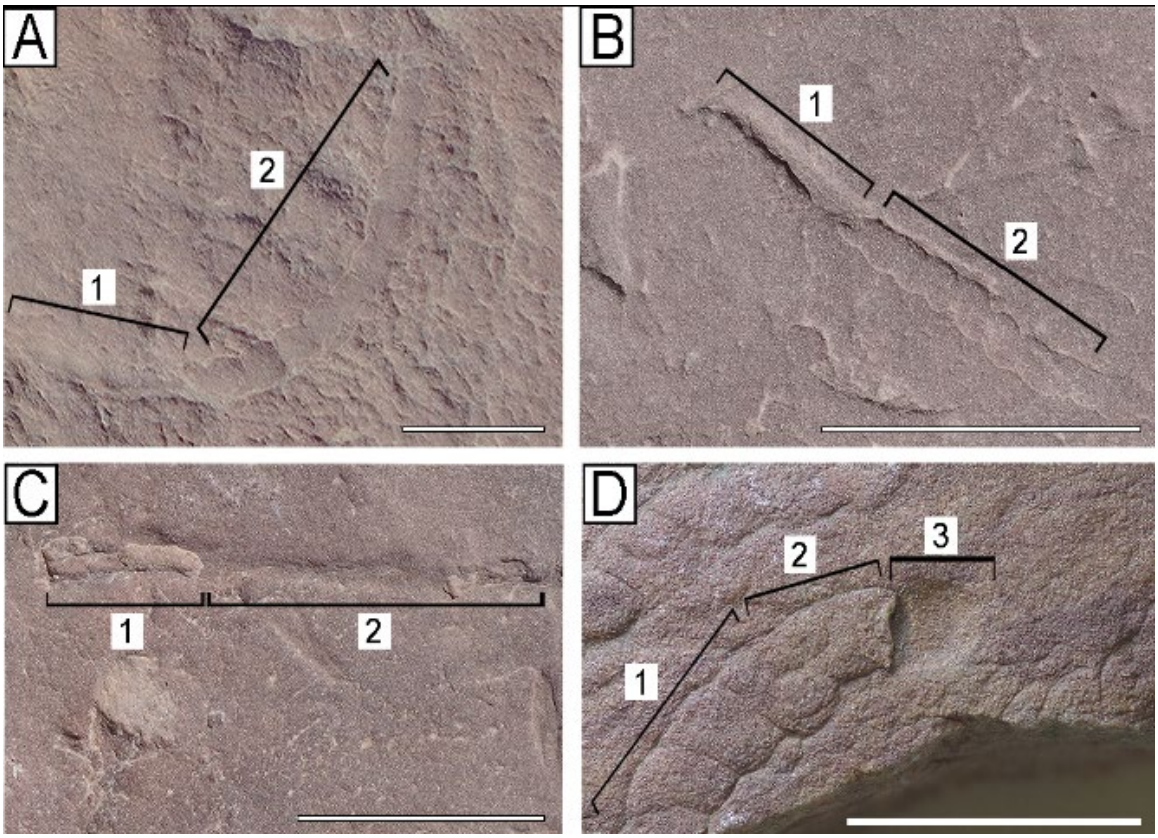


FIGURE 4 — Multi-part preservation of *Funisia dorothea*. **A)** Negative relief external mold (1) and positive relief external mold (2); scale=3.5 cm **B)** Negative relief internal mold (1) and positive relief external mold (2); scale=1.5 cm. **C**) Positive relief internal mold (1) and negative relief internal mold (2); scale=1.5 cm. **D)** Positive relief external mold (1), positive relief internal mold (2), and negative relief external mold (3); SAM F17032; Scale=1.5 cm.

Taphonomic grade 1 (TG 1) represents the highest level of detail preserved in *Funisia*, including defined serial modularity (e.g., Table 2: Taphonomic Grade 1).

Taphonomic grade 2 (TG 2) defines an external mold that does not preserve serial modularity but exhibits defined scalloped lateral margins (e.g., Table 2: Taphonomic Grade 2). Taphonomic grade 3 (TG 3) is defined by lower preservational fidelity, with lateral margins of the *Funisia* presenting as irregularly undulating lines without serial modularity and poorly defined or absent scalloping (e.g., Table 2: Taphonomic Grade 3). Taphonomic grade 4 (TG 4) is the most degraded taphomorphic variant of *Funisia* and is defined by fully negative relief preservation of a lenticular groove with parallel lateral margins terminating in an acute angle at either end (e.g., Table 2: Taphonomic Grade 4). This taphonomic grade, first described as an iterative organosedimentary textured organic surface (TOS) named "groove" (Gehling and Droser 2009), is distinct from both aforementioned negative relief *Funisia* preservational types (e.g., external and internal molds) in that it is a *Funisia*-generated sedimentary structure produced by the complete degradation of associated positive relief external molds. Because "groove" (referred to as TG 4 for the remainder of this discussion) represents an end-member of *Funisia* external mold preservation, indicating complete degradation of *Funisia* integument, it is included as a part of the taphonomic grade scale.

The relative abundances of *Funisia* taphomorphs on each bedding plane were used to place each *Funisia*-dominated bedding plane within taphospace on a ternary taphogram to establish a semi-quantitative basis for the interpretation of biostratinomic mechanisms of variability among *Funisia* populations (Table 2).

In the process of preservational mode and taphonomic grade recognition, differentiation between similar forms with distinct biostratinomic implications was

important. This was as a primary concern for the differentiation between positive relief internal molds (Fig. 3C) and TG 3 external molds (Table 2), as well as negative relief internal molds (Fig. 3D) and TG 4 external mods (Table 2). In the case of distinguishing between positive relief internal molds and TG 3 external molds, neither of which preserve modularity, the two forms are reliably distinguished based on the presence or absence of textural disparity between the fossil and the bedding plane associated with the interpolation of the *Funisia* integument (Fig. 3C, Fig. 4C, 4D). In the case of internal molds, the *Funisia* integument serves as an organic barrier between the sediment infill and the overlying and encasing sand body deposited during the final burial event, resulting in a visible distinction between the infill and the bedding plane (Fig. 3C). In contrast, positive relief external molds result from the collapse of the tube body and subsequent molding of the exterior. As such, the molding sediment and encasing sand body are one-in-the-same (i.e., not separated by an organic barrier), resulting in no textural disparity with the associated bedding plane (Fig. 3A).

Distinguishing negative relief internal molds from TG 4 *Funisia*, is more complex in that both forms express as concave taphomorphs with few morphological characters. Negative relief internal molds reflect the presence of an infilled body cavity upon burial that is subsequently lost (the mechanisms behind which is not fully understood, but follows logic of organic surfaces serving as barrier to amalgamation of synlithological bedforms (Tarhan et al. 2015)) (Fig. 3D) and TG 4 represents the molding of organically mediated sedimentary structures (Table 2: taphonomic grade 4). Therefore, textural disparity cannot be used to distinguish between the two forms, but their differentiation is

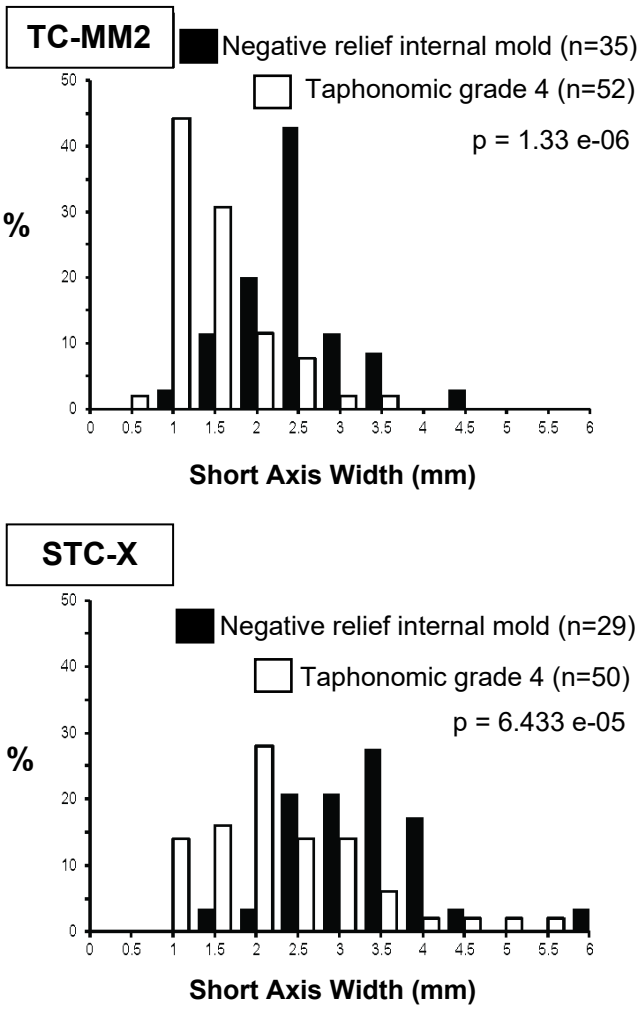


FIGURE 5 —Short axis width distributions of visually identified "groove" structures and negative relief internal molds on bedding planes TC-MM2 and STC-X. P-values report results from Kolmogorov-Smirnov two sample t-test of the size distributions ($\alpha = 0.05$).

essential as they represent distinct biostratinomic processes. In the field, morphological criteria were used to define the difference between these two forms. Negative relief internal molds were characterized by terminations in blunt, parallel to sub-parallel margins (arrows in Fig. 3D). TG 4 was characterized by lenticular negative relief structures with inversely scalloped margins (Table 2) and acute terminations. When using these qualitative criteria to differentiate between negative relief internal molds and TG 4, the two forms should exhibit distinct short axis width distributions due to their discrete formation mechanisms, that is, internal molds should roughly mirror width distributions of *Funisia* external molds, whereas the sedimentary structures represented by TG 4 should be distinct. To test whether the proposed morphological criteria reflect distinct structures, the widths of negative relief internal molds and TG 4 structures were

measured across two *Funisia*-dominated beds that are characterized by these two preservational forms (Fig. 5). Resulting short-axis distributions show visually distinct size distributions for the two forms, and when subjected to a Kolmogorov-Smirnov two sample t-test (chosen because it is a widely invoked test for the comparisons of quantitative variables) the null hypothesis that both samples come from the same distribution can be rejected (see p-values Fig. 5). The resulting statistically distinct distributions confirm the biostratinomic distinction between these two structures and provide confidence in the use of the identified morphological characteristics to differentiate between the two preservational forms.

RESULTS

Funisia populations at Nilpena occur in two primary assemblage types:

1. Cluster-type assemblages: characterized by multiple distinct stands of relatively low-density *Funisia* clusters with well-preserved external features (e.g., modularity) − each covering no more than 0.5 m^2 and separated by non-*Funisia* bearing textured organic surfaces and macrobiota (Fig. 2B, 2D, 2F).

2. Surface-type assemblages: characterized by densely overlapped and generally poorly preserved *Funisia* covering > 90% of the fossiliferous surface (Fig. 2A, 2C, 2E).

Two beds at Nilpena are characterized by cluster-type *Funisia*, referred to as TB-BRW and LV-FUN, located in the ORS and PLRUS facies respectively (Table 1). Five fossiliferous surfaces are characterized by surface-type preservation of *Funisia*: TC-MM2, STC-Maws, STC-X, WS-MAB, and WS-JDB (Table 1). In surface-type and cluster-type assemblages positive relief external molds (Fig. 3A) make up 71% of all

preserved *Funisia,* making it the most commonly observed preservational mode in *Funisia* populations at Nilpena as a whole.

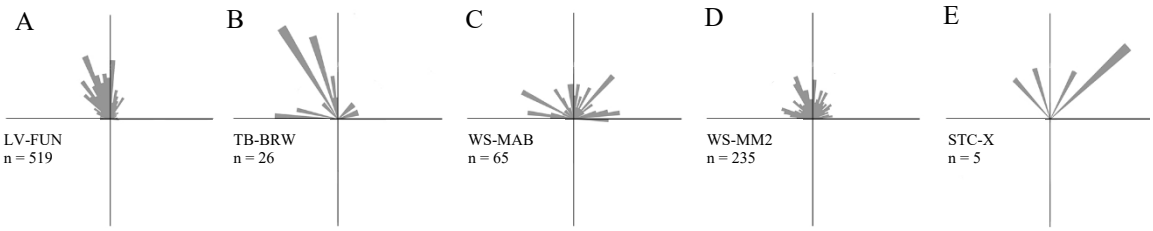


FIGURE 6 — Orientation of Funisia populations across all Funisia-dominated, reconstructed bedding planes. **A**) LV-FUN. **B**) TB-BRW. **C**) WS-MAB. **D**) WS-MM2. **E**) STC-X. Figure made using Stereonet 10 (http://www.geo.cornell.edu/geology/faculty/RWA/programs/*stereonet.html).*

Interpretation of these packing modes as well as their biostratinomic and paleoecological implications are dependent on the observed communities representing *in situ* (not transported) assemblages. In both surface- and cluster-type assemblages *Funisia* do not exhibit strong current alignment (Fig. 6), and the wide distribution of orientations is not consistent with current-impact and/or transported assemblages (Tarhan et al. 2010; Evans et al. 2015).

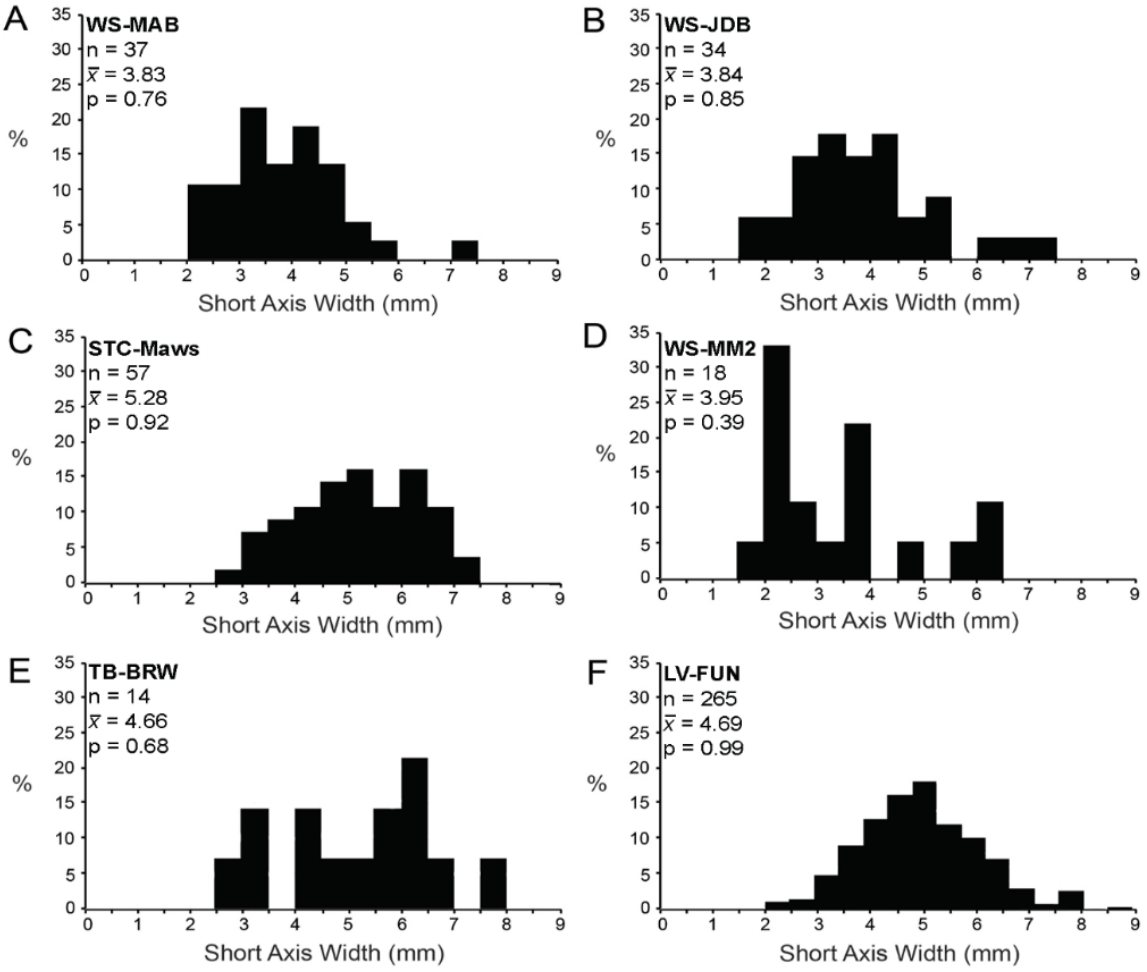
With no evidence of transport observed, discrete bedding planes can be interpreted as *in situ* populations, allowing for size distributions to provide biologically meaningful insight into *Funisia* reproduction and life mode. We report the cumulative frequency distributions of *Funisia*-dominated bedding planes (Fig. 7) using only specimens preserved as external molds that retain modularity (i.e., TG 1 and 2) to minimize deformation bias that is inherent with collapsed soft-bodied organisms. A draw-back to using only the best persevered specimens is that it yields a small sample size for most bedding planes and eliminated the use of STC-X because it is dominated by TG 4.

Due to this small sample size, short-axis width distributions of *Funisia* populations exhibit non-uniform distributions (Fig. 7A, B, D, E), though beds with larger samples sizes approach unimodality (e.g., Fig. 7C, F). To address the potential of multimodality in the size distributions with smaller sample sizes, Hartigan Dip tests of multimodality were run for each distribution (Hartigan and Hartigan 1985). The resulting p-values (reported on Fig. 7 histograms) are high for all beds, thus not allowing for the rejection of the null hypothesis of unimodality and providing no evidence for multimodality in any of the bed-scale *Funisia* populations.

To assess the variability in short-axis width distributions between populations, size data was subjected to pairwise comparisons using Kolmogorov-Smirnov two sample t-tests (Fig. 7G), half of the comparisons of size distributions exhibit significantly different mean sizes whereas the other half of the comparisons cannot be distinguished.

Taphonomic Grades

All four *Funisia* taphonomic grades are observed in both the ORS and PLRUS facies on bedding planes dominated by both cluster- and surface-type *Funisia* populations. However, the ratios of taphonomic grades on discrete bedding planes vary notably relative to each other. *Funisia*-dominated beds do not all cluster together in taphospace but reveal some degree of nuance to the state of *Funisia* degradation (as indicated by the dominant taphonomic grade). Multiple clusters of bedding planes are observed, but these groups cannot be described by facies association alone, thus indicating a degree of non-facies based preservational variability (Table 2).



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	WS-JDB	STC-Maws	TC-MM2	TB-BRW
WS-MAB	p = 0.95 D = 0.13	p < 0.0001 D = 0.57	p = 0.80 D = 0.19	p = 0.02 D = 0.48
LV-FUN	p = 0.001 D = 0.37	p = 0.02 D = 0.23	p = 0.03 D = 0.36	p = 0.33 D = 0.27
WS-JDB	–	p < 0.0001 D = 0.53	p = 0.91 D = 0.17	p = 0.08 D = 0.42
STC-Maws	–	–	p = 0.001 D = 0.53	p = 0.58 D = 0.24
TC-MM2	–	–	–	p = 0.24 D = 0.38

FIGURE 7— Cumulative frequency distributions of tube widths (TG 1 and 2) on *Funisia*-dominated bedding planes. P-values reported on plots are results from Hartigan Dip Tests for multimodality (α = 0.05). **A**) WS-MAB. **B**) WS-JDB. **C**) STC-Maws. **D**) WS-MM2. **E**) TB-BRW. **F**) LV-FUN. **G**) Results from Kolmogorov-Smirnov two sample t-tests of size distributions, bolded cells correspond to cross-facies comparisons (α = 0.05).

DISCUSSION

Taphonomic Grades

The definition of taphonomic grades 1-3 is relatively straightforward in that a specimen's rank is defined based on the presence or absence of modularity and lateral scalloping in individual *Funisia* (Table 2).

However, the final taphonomic grade, TG 4, warrants further discussion. Our proposed definition of the previously named "groove" TOS (Gehling and Droser 2009) as a sedimentary structure created through the degradation of *Funisia* surfaces is the result of observations collected from multiple *Funisia*-dominated bedding planes across two facies. This large and diverse dataset provides a combination of depositional environments and biostratinomic conditions that have allowed for the identification of a continuum of *Funisia* preservation that predicts TG 4 as a necessary and expected preservational end-member of *Funisia.* However, we recognize that assigning a precursor taxon to a TOS comes with many assumptions and could easily be deemed to be a creative conjecture. However, there are multiple lines of evidence that support our interpretation:

1. Occurrence of TG 4 in densely packed, high abundance populations covering entire bedding planes–a characteristic that, within the discrete macrobiota at Nilpena, is unique to *Funisia* (Fig. 8A).
2. Observation of TG 4-dominated surfaces laterally transitioning into patches of distinct well-to moderately-well preserved *Funisia* on beds dominated by "groove" structures (i.e., STC-X).

3. Ubiquitous association of TG 4 with discrete *Funisia* fossils, indicative of an intimate association between the two.
4. Common association of TG 4 with TG 2 and TG 3 *Funisia*, occurring parallel or sub-parallel to the lateral margins of "groove" structures (Fig. 8D, 5E). While it could be suggested that this association does not necessitate *Funisia* as the mechanism of TG 4 formation but could instead reflect the current-mediated alignment of *Funisia* with the high relief groove structures, we do not observe evidence consistent with this idea. The few TG 2-3 *Funisia* recorded on bed STC-X, the one bed dominated by TG 4, do not exhibit current alignment (Fig. 6E), and there are no examples of *Funisia* wrapped around groove structures as would be expected if this association was simply the result of transported *Funisia* trapped by the high relief groove structures. This is particularly insightful when considering *Funisia's* relationship with *Aspidella*, wherein we commonly observe TG 3 *Funisia* wrapping around the margins of *Aspidella* (Fig. 2C). If this is an expected reaction of felled *Funisia* to obstacles, there is no reason why it should be absent on STC-X if the association of TG 4 with *Funisia* is simply due to current-related buildup of organic material around unrelated high relief structures.
5. The observed overlap of mobile macrobiota (e.g., *Dickinsonia*) with TG 4, exhibiting morphological disturbance from the underlying surface, indicative of TG 4 being a resistant, sessile surface feature of relatively high relief (Fig. 8B).
6. The placement of other immobile macrobiota (e.g., *Rugoconites*, *Parvancorina*) exclusively between TG 4 structures, suggesting a resistance of these organisms to

settling on top of a high relief structure (Fig. 8C).

Following these lines of evidence, we propose a hypothetical process of TG 4 formation, which begins with the felling and non-burial of densely packed *Funisia* (Fig. 9B). This initial step already distinguishes TG 4 dominated beds from all other surface-type *Funisia* beds discussed herein because time of burial is not equivalent to the time of death for TG 4-dominated fossil surfaces. In the context of the episodic burial events and the absence of widespread scavenging that characterizes the Ediacara Member, the

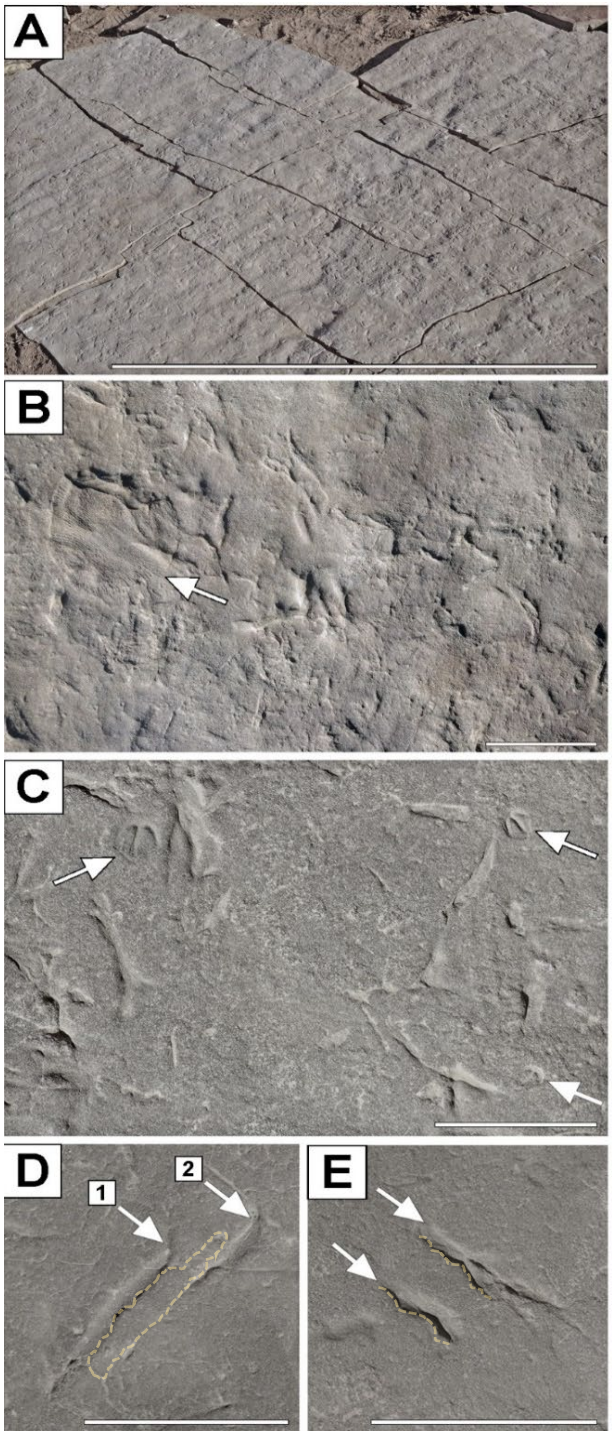

FIGURE 8 — Examples of TG 4. **A**) Bedding plane STC-X, abundance of TG 4 creates a TOS; scale = 1 m. **B**) TG 4 surface with overlain and deformed *Dickinsonia* (arrow); scale=5 cm. **C**) TG 4 surface with *Parvancorina* (arrows) located between grooves; scale=3 cm. **D**) Positive relief external mold (TG 3) (outlined) paralleled by two "groove" structures (arrows 1 and 2); scale=3 cm. **E**) Two "groove" structures (white arrows) with no associated discrete *Funisia*, but inverse scalloping is present along long-axis margins (outlined); scale=5 cm.

deceased *Funisia* would, presumably, have remained at the sediment-water interface as a high relief organic layer for an ecologically significant period of time as decay took place.

This unburied *Funisia* death assemblage would have functioned as a TOS, allowing for the re-colonization of the seafloor by Ediacara macrobiota in the absence of resource competition from living communities of *Funisia* (e.g., Fig., 9A), as well as allowing for the buildup of sediment between and on top of the collapsed *Funisia,* gaining higher relief at points of tube overlap which potentially created ridges of integument between felled *Funisia* (Fig. 9D-F). In conjunction with sediment build-up was the

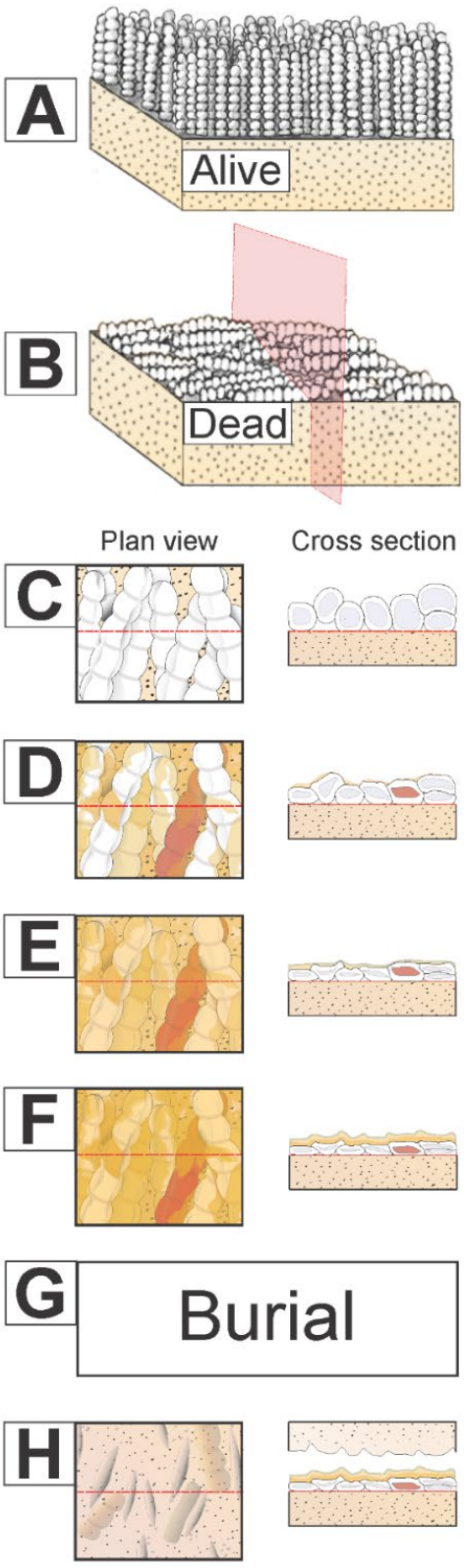

FIGURE 9— Illustration of the progressive formation of "groove" structures. Left column represents plan-view of felled *Funisia*. Right column represents cross-section of the transect indicated by the red box in part B and the red dashed line in plan view. **A**) Living *Funisia* community. **B**) Death and non-burial of *Funisia.* **C)** Newly felled *Funisia*. **D**) *Funisia* has begun to collapse, infill, and be covered by sediment. **E**) The degradation process continues, and sediment builds up further. **F**) Continued degradation, collapse, and sedimentation. **G**) Final burial of the degraded *Funisia* surface. **F**) The resulting fossiliferous surface.

probable recurrent growth or regrowth, alternating with sedimentation, of microbial surfaces on top of the sediment accreting on and between *Funisia.*

This microbially-bound sediment would have, overtime, formed increasingly high-relief and resistant structures between dead and collapsed *Funisia* tubes (Fig. 9F). Upon final burial of this surface, the resistant sediment ridges would have created negative-relief lenticular grooves, whereas the degraded *Funisia* were only rarely preserved as discrete tubes (Fig. 8A, 8B; Fig. 9H). The resulting TG 4-dominated fossiliferous surface would represent a time avergaed *Funisia* assemblage, serving as an expected taphonmic end-member of preservation wherein complete degradation of *Funisia* integument has occurred.

Paleoecology

Funisia populations at Nilpena are found to have had a single life habit characterized by the dense packing of abundant individuals. Whether covering entire bedding planes as surface-type populations (Fig. 2A,C,E) or appearing as several groups distributed across a bedding plane as cluster-type assemblages (Fig. 2B,D,F), *Funisia* are consistently found as dense aggregates, supporting a model of ubiquitous close-packing of *Funisia* populations. This life habit allowed for the unique abundance of *Funisia* within the Ediacara Member (Table 1), which in turn is liable to have had important paleoecological implications.

However, interpretations of *Funisia's* role in community ecology cannot be carried out without assurance that *Funisia*-dominated bedding planes represent *in situ*

communities. Evidence from bed-scale observations supports the *in situ* preservation of all observed *Funisia* communities at Nilpena (Fig. 6), and the potential for these populations to represent size-similar (unimodal) cohorts cannot be rejected based on tests of multimodality (Fig. 7). This indicates that the non-uniform appearance of *Funisia* size distributions is not indicative of a non-unimodal distribution but is most likely a consequence of small sample size, as TG 1 and 2 *Funisia* are quite rare.

The model of all autochthonous *Funisia* populations occurring in comparably densely packed, size-similar cohorts is further supported by the distribution of discoid holdfast structures associated with *Funisia* body fossils (Fig. 10). These structures are preserved as positive hyporelief concentric circles in generally densely packed, size-similar cohorts (Fig. 10B). Holdfasts are not common, presumably because their preservation

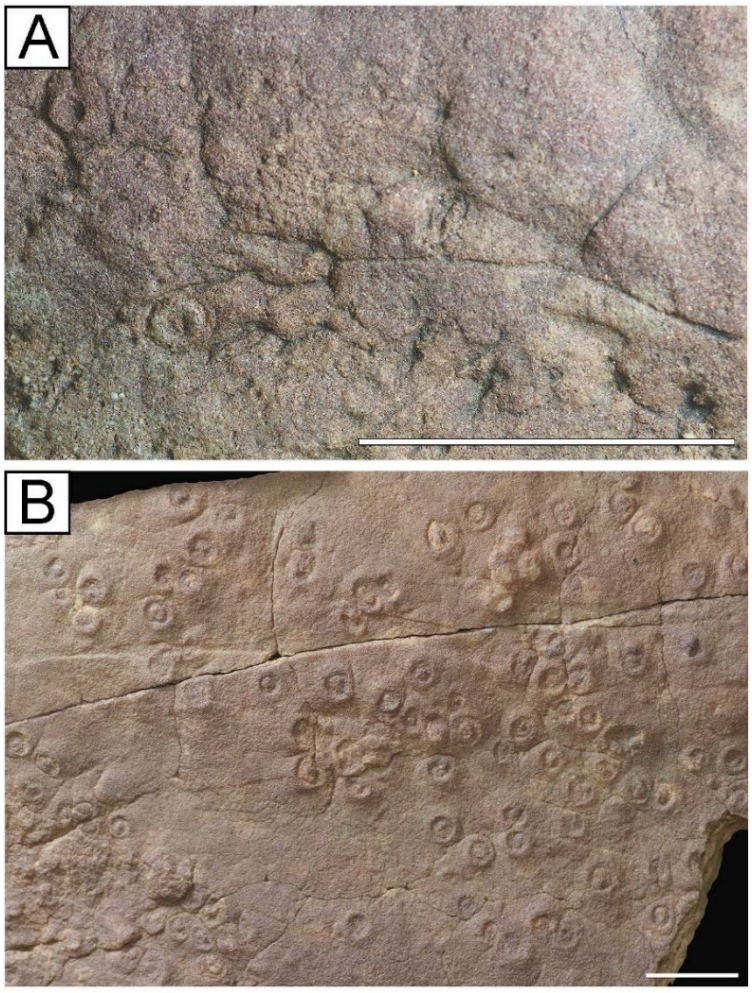

FIGURE 10—Images of *Funisia dorothea* holdfast structures. **A**) Taphonomic grade 3 *Funisia* tube attached to holdfast; SAM P42681. **B**) Densely packed holdfasts; SAM P55236. All scales = 1.5 cm.

necessitated the severing of the upright *Funisia* tube and the subsequent infill of remaining holdfast structure that was rooted beneath the mat surface (Fig. 11A). Given the common occurrence of large *Funisia* populations preserved as *in situ* populations, with preserved evidence for the severing and the transport of tubes being rare, the biostratinomic scenario required for holdfast preservation is not expected to be common. However, because holdfasts are necessarily preserved *in situ*, these structures provide unequivocal evidence of living *Funisia* occurring solely in dense, size-similar clusters.

Additionally, distinctions in size distributions between bedding planes do not have a clear mechanism, as they do not reflect facies associations or other known biostratinomic factors (Fig. 7G). This is consistent with interpretations of *Funisia*-dominated beds as distinct cohorts in different growth stages. While facies association does not appear to have an effect on size distributions, the LV-FUN size distribution is distinct from all other bedding planes except for TB-BRW. These bedding planes are the only two cluster-type assemblages, suggesting a potential connection between packing type and population size distributions that warrants further investigation.

In sum, this evidence supports initial interpretations of *Funisia* as an organism that reproduced via spatfall, creating a series of limited size-similar cohorts suggestive of sexual reproduction (Droser and Gehling 2008). However, the poor preservational quality of the majority of currently excavated *Funisia* populations thus far precludes a definitive interpretation.

This life mode may explain *Funisia's* observed associations, or lack-there-of, with other organisms. On beds preserving non-time averaged surface-type *Funisia*

assemblages, which is the most common *Funisia* packing type at Nilpena, taxonomic diversity is low and the only other common *in situ* organism associated with *Funisia* is *Aspidella*, which is generally well-preserved (Fig. 2C) (Tarhan et al. 2015). The association of surface-type *Funisia* alongside well-preserved *Aspidella* is observed on the majority of beds dominated by *Funisia* packages and represents one of two repeating biofacies (the other being dominated by *Plexus ricei* and *Phyllozoon* (Droser et al. 2019)) at Nilpena, which is otherwise characterized by considerable inter-bed heterogeneity in community structure (Droser et al. 2019; Finnegan et al. 2019). Significantly, this biofacies is characterized by well-preserved *Aspidella* and poorly preserved (i.e., TG 2 and 3) *Funisia*, suggesting that dense *Funisia* populations served as a sediment stabilizer that prevented the plucking and/or collapse of *Aspidella* that is common on other beds that are not dominated by *Funisia* (Tarhan et al. 2010). In the rare instance that an organism other than *Funisia* or *Aspidella* is preserved on surface-type bedding planes, the organisms consistently show evidence of transport and are generally mobile or planktonic organisms (e.g., *Spriggina*, *Dickinsonia*). This is significant in that organisms with these life habits could have easily been suspended in the water column at the time of burial or could have been swept in due to their non-anchored life habit. It is, therefore, evident that in life *Funisia* played a critical role in ecosystem dynamics, primarily in the form of restricting regional recruitment of taxa with epibenthic life habits and as a taphonomic influencer through the stabilization of sediment.

Bedding planes dominated by cluster-type *Funisia*, however, do not exhibit the same associations with *Aspidella* and generally have higher evenness, showing

association with well-preserved mobile and sessile macrobiota as well as non-*Funisia* TOS. This is consistent with the interpretation of surface-type *Funisia* preventing colonization through resource sequestration. In contrast, cluster-type *Funisia* leave large areas of the seafloor unoccupied, allowing for further colonization. However, on these beds *Funisia* remain the most abundant organism due to their close-packing tendencies.

Further, we observe a unique association of the one bedding plane dominated by TG 4 (STC-X) (Table 2) and higher bed-scale diversity. Taphonomic evidence allows for the interpretation of TG 4 surfaces as time averaged communities, wherein the preserved surface represents a community of organisms living on top of a deceased *Funisia* population (Fig. 8B,C). In this instance, STC-X is defined as a surface-type *Funisia* community. However, STC-X represents an unburied death assemblage, leading this *Funisia* population to function not as a group of discrete macrobiota sequestering resources, but as a TOS that potentially provided a food source for other macrobiota. Importantly, *Funisia* is the only recorded eukaryote-grade TOS creator, which are otherwise characterized by less complex prokaryote-grade populations (Gehling and Droser, 2009). Therefore, while it is clear that surface-type *Funisia* inhibited seafloor colonization in life, in death they appear to have facilitated colonization. This dual paleoecological role is unique to *Funisia* within the discrete macrobiota of Nilpena and can be directly attributed to its characteristically high abundance.

Biostratinomic Controls

Of the four preservational modes that define *Funisia,* positive relief external molds −representing the collapse of a tubular body− are the most abundant (representing 81% of all *Funisia* recorded in bed-scale observations). Importantly, this abundance of collapsed external molds, which record successive losses in character definition, provides insight into the biostratinomic mechanisms behind the surprising variability in community-scale preservation of *Funisia* between bedding planes.

However, before interpreting bed-scale preservation of *Funisia* communities, we can identify several trends in taphomorph representation. The most common taphonomic grade observed across all bedding planes is TG 3, with TG 1 being the rarest. This indicates that regardless of biostratinomic conditions, *Funisia* preferentially lost module definition upon death and collapse. This not only holds implications for *Funisia* structure but also indicates that presence or absence of well-preserved *Funisia* (e.g., TG 1 or 2) is not necessarily a useful marker of rapid preservation under ideal conditions. Instead, it is clear that even under good preservational conditions, a large number of specimens will not preserve modularity. Additionally, when bedding planes are placed within comparative taphospace based on the relative representation of taphonomic grades, we observe patterns in *Funisia* preservation that go beyond simple collapse-related deformation of soft-bodied organisms. Based on clustering patterns of beds in the ternary taphogram (Table 2) we can identify several higher order patterns in *Funisia* preservation, with visible groups forming based on *Funisia* package-type, time averaging, and, to a lesser degree, facies association (Table 2).

Of all seven *Funisia*-dominated bedding planes, the populations that preserve the highest-detail *Funisia* populations are the cluster-type assemblages (i.e., LV-FUN and TB-BRW) (Table 1; Table 2). This packing-based grouping spans ORS and PLRUS facies, indicating that the extent of individual packing had more of an effect on overall *Funisia* preservation than did facies association. This is broadly indicative of *Funisia* overlap and composite preservation resulting in more frequent module degradation. However, the distribution of surface-type assemblages within taphospace cannot be described solely by packing-type, with three distinct bedding plane groups forming: (1) WS-MAB and WS-JDB, (2) TC-MM2 and STC-Maw, and (3) the isolation of STC-X (Table 2).

It appears that, in contrast to cluster-type assemblages, surface-type assemblages are defined by their facies association. Beds hosting surface-type assemblages located in the PLRUS facies cluster together (WS-JDB and WS-MAB) and record a high percentage of TG 3 *Funisia*. Beds located in the ORS facies (TC-MM2 and STC-Maw) display lower numbers of TG 3 *Funisia*, with TG 1 and 2 representation nearing that of cluster-type assemblages (Table 2). This is, presumably, the result of differential energy regimes. PLRUS surfaces exhibit lower detail preservation because of the higher energy conditions in planar laminated regimes; ORS packages are preserved in higher detail as a result of the lower energy, oscillatory conditions. Importantly, these variable energy conditions do not impact cluster-type assemblages, suggesting that energetic conditions play a lesser role in *Funisia* preservation potential than does packing.

The final variable that is explanatory of the patterns observed in the ternary taphogram distinguishes between STC-X and the six other *Funisia*-dominated bedding planes. This reflects the dominance of TG 4 on bedding plane STC-X, which can be attributed to the amount of time between the death of the *Funisia* community and final burial of the surface.

In sum, the placement of *Funisia*-dominated beds within taphospace indicate that package-type and the extent of time averaging served as first-order controls on *Funisia* preservation, with facies association being related but not serving as a primary biostratinomic filter.

Morphology

The hollow body and external serial modularity of *Funisia* is well constrained based on previous observations of abundant, high detail external molds with evidence of collapse-induced wrinkling, as well as the presence of partial internal molds (e.g., Fig. 3C) (Droser and Gehling 2008). Further support for a fluid-filled body cavity is presented by *Funisia's* diversity of preservational modes defined herein, which provide evidence of an organism whose structure allowed it to differentially withstand burial without collapse (negative external mold), to collapse upon burial (positive external mold), or to infill with sediment (positive/negative internal molds). A fluid-supported integument would have, presumably, allowed *Funisia* to resist collapse and deformation in life or in rare instances when fluid was trapped inside of the tube by the casting event, resulting in a negative external mold (Fig. 3B). Simultaneously, this body structure would have made it so that fluid could be released from the body cavity upon death, resulting in complete loss of the

tubes structural integrity and variable loss of modularity (e.g., positive external mold), or infilling of the body cavity (e.g., internal molds) (Fig. 3A, C-D).

This model helps to elucidate the mechanism behind *Funisia's* ability to live upright, extending up to 30 cm into the water column (Droser and Gehling 2008), despite having a flexible, non-rigid integument. Taphonomic evidence suggests that *Funisia* integument was robust and was able to maintain support of the *Funisia* body through internal fluid-derived rigidity, not through the support of an air bladder (e.g., as in living kelp) (Fig. 11B-D).

No evidence for the presence of modules on the internal body wall of *Funisia* is observed. Internally molded *Funisia* of both positive and negative relief never preserve modularity, suggesting a lack of preservable internal characteristics. The ubiquitous absence of modularity in internally molded specimens, however, does not preclude the potential of internal modularity with low preservation potential. For this reason, our reconstruction of *Funisia* morphology illustrates both potential scenarios (Fig. 11C). These observations provide no evidence for a tube-in-tube structure as is proposed for other tubular taxa outside of the Ediacara of South Australia (Chen et al. 2008). Instead, we propose a model of *Funisia* in which a relatively thick integument composed of successive modules (Fig. 11B-C) encloses a fluid-filled body cavity (Fig. 11D). This interpretation is consistent with previous descriptions of *Funisia* as a poriferan- or cnidarian-grade organism (Droser and Gehling 2008).

In previous publications *Funisia* was modeled to have grown via terminal addition of modules (Droser and Gehling 2008). This interpretation is consistent with

taphonomic evidence presented herein and with the proposed body structure of *Funisia* (Fig. 11E). We model this hypothetical process as the budding and expansion of new modules on the apical end of *Funisia* tubes with progressive expansion of the hollow body cavity. While consistent with observations at Nilpena, this growth model represents a hypothetical scenario based on known growth processes in modern metazoans, though newly excavated material may provide more substantial results in the future.

Several inferences about integument strength in addition to morphology can be made based on observation of *Funisia's* preservational variability. Several *Funisia* specimens at Nilpena suggest that it was flexible both when fluid-filled and after collapse, enabling it to bend without rupturing (Fig. 12B,C). *Funisia* is found preserved as negative relief external molds bent at acute angles, suggesting that despite the sharp bending of a fluid-filled, rigid *Funisia*, it was not immediately prone to rupture (Fig. 12C).

Additionally, positive relief external molds are frequently bent at obtuse to acute angles. This flexibility was apparently only exploitable to an extent, after which tubes either collapsed or infilled as a result of ripped or ruptured integument (e.g., positive external mold and internal molds). The negative relief external mold preservational mode (Fig. 3B) of *Funisia* reflects the burial of *Funisia* without deflation of the body cavity, therefore reflecting the tubes strength in life. In this scenario, the retention of internal fluids allows *Funisia's* external surface to be molded as a resistant structure resulting in a negative relief fossil. It is important to note that this preservational mode is notably rare

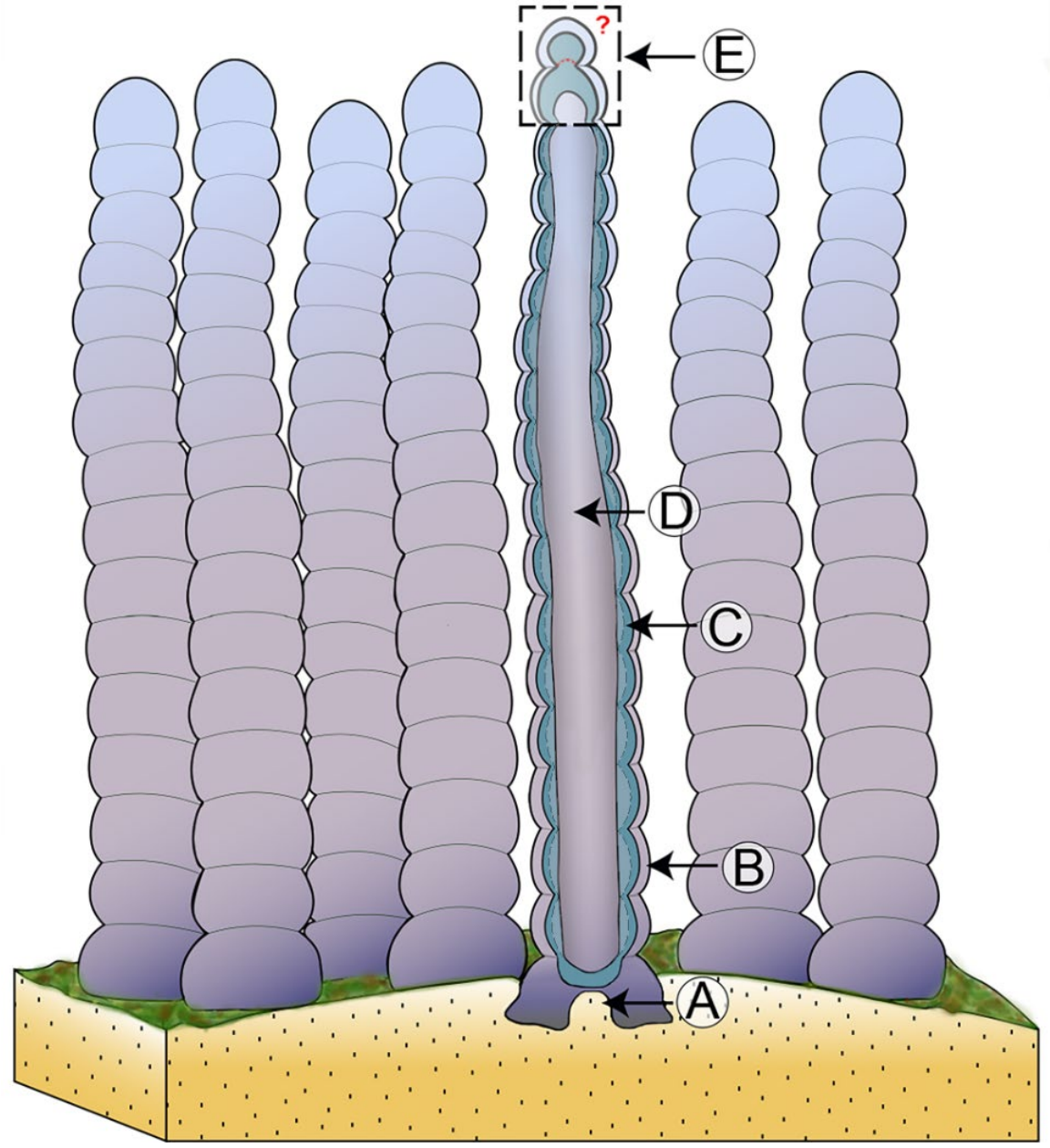

FIGURE 11 — Illustration of *Funisia dorothea* cluster in life and a hypothesized cross-sectional anatomy. Tube decreases in width towards the apical end, indicative of growth via terminal addition of modules **A**) Holdfast. **B**) Outer wall of the *Funisia* body, exhibiting modularity. **C**) Inner wall of the *Funisia* body, no modularity present. **D**) Hollow, fluid-filled interior of *Funisia*. **E**) Hypothesized growth process of *Funisia* (represented by opaque box). Modules begin as small buds on the apical end of the tube, red dotted line represents nucleation point. New modules are hypothesized to originate as non-hollow modules followed by successive expansion of the integument and hollow body cavity.

in comparison to the abundant positive relief external molds, suggesting that retention of fluid was uncommon.

Importantly, negative relief external molds always preserves modularity and do not exhibit sequential degradation of modularity as do positive relief external molds. As such, *Funisia* appears to have maintained strength and buoyancy as well as a degree of flexibility (Fig. 12C) through its fluid-filled internal cavity. This relationship between module retention and fluid retention further suggests that *Funisia's* structural integrity and ability to stay upright in the water column was largely derived from its hollow, fluid-filled (i.e., saline) body cavity.

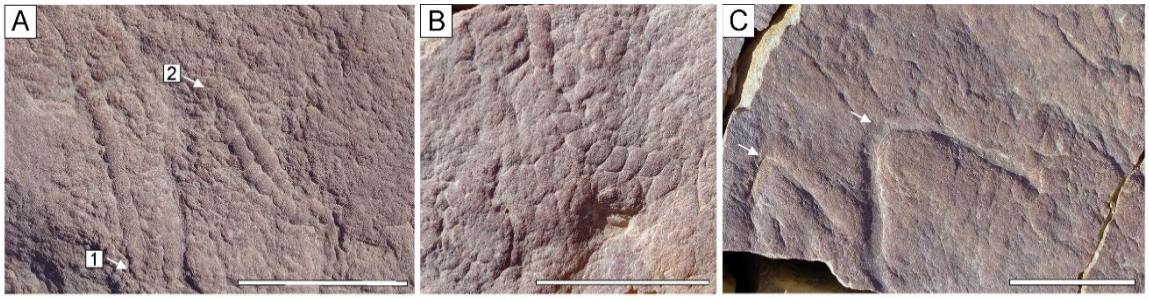

FIGURE 12—Images of *Funisia dorothea* exhibiting bending and characteristic terminations. **A)** Taphonomic grade 1 *Funisia* with blunt terminating ends (arrows 1 and 2); scale = 5 cm. **B**) Obtusely bent *Funisia*; scale = 3.5 cm. **C**) Acutely bent negative relief external molds of *Funisia*; scale = 5cm.

The formation of positive relief external molds is proposed to have occurred as a pre- or syn-depositional form of deformation, wherein this fluid is lost from the *Funisia* body cavity, resulting in the preferential deflation of the tube and common loss of modularity in the resulting mold (Droser and Gehling 2008). This implies that upon the loss of its internal fluid, the preservation potential of *Funisia* external integument decreased. This interpretation is additionally consistent with TG 3 being the most

commonly observed taphonomic grade of positive relief external molds. Therefore, we see that in life *Funisia* maintained a degree of strength whereas in death, structural integrity was rapidly lost. Somewhat counterintuitively to *Funisia's* tendency to collapse, is the absence of preserved rips or ruptures in *Funisia* integument. This is further indicative of a body-wall with an ephemeral integrity that, once ruptured, experienced an immediate decrease in preservational fidelity, preventing the preservation of partially ripped modules or distinctly ruptured edges. Instead, collapsed *Funisia* exhibit only moderate wrinkling of modules that always terminate in blunt ends representing complete modules (e.g., Fig. 12A arrows 1, 2).

The sum of this evidence suggests that *Funisia* integument was strong enough in life to create negative molds with clear modularity (e.g., negative relief external molds) (Fig. 3B), but weak enough upon death and collapse to preferentially lose module definition in positive relief external molds (e.g., Table 2), as well as to prevent the preservation of distinctly ripped edges. Significantly, even in high-detail cluster-type assemblages that preserve a relatively high number of TG 1 and 2 tubes (e.g., TB-BRW and LV-FUN), taphonomic grades with distinct modularity do not make up more than ~50% of the total taphomorph compositions (Table 2). This trend speaks to how readily *Funisia* lost modularity after death, suggesting some form of immediate tissue collapse upon release of the internal fluid.

This biomechanical response to deformation is unique to *Funisia* among modular organisms preserved in the Ediacara Member. Such collapse and loss of modularity is not observed in other modular organisms such as *Dickinsonia*, which maintain a resistant

structure and modularity even upon death, transportation, and deformation (Evans et al. 2019b). This distinction can be attributed to the hollow body form of *Funisia*, suggesting that this pattern in preservational variability and predictability could provide a taphonomic framework for the broader characterization of tubular organisms as a group, which are united by their hollow bodies and complicated preservation.

CONCLUSION

Funisia is the most abundant body fossil preserved in the Ediacara Member, yet its significance and function as a part of Ediacara ecosystems has, thus far, remained poorly constrained due to the taxon's simple, hollow body plan and densely packed life habit—features that additionally contributed to complex and poorly understood taphonomic variability. This treatment of *Funisia* biostratinomy is essential to understanding critical aspects of Ediacara ecology, including non-artefactual species-level diversity, inter-bed heterogeneity, and ecosystem dynamics. Additionally, the characterization of *Funisia's* taphonomic variability has implications for the accuracy of previously established preservational models of Ediacara-type mold and cast preservation (e.g., MacGabhann et al. 2019), and whether these preservational models can be accurately applied to the siliciclastic setting of the Ediacara Member.

With knowledge of the impacts of *Funisia's* body structure on overall preservation of *Funisia* communities, the relative impact of other biostratinomic factors (e.g., paleoecology and sedimentology) on the preservational state of *Funisia* surfaces can be assessed. Specifically, the close packing of *Funisia*, as well as the energy of the system in which they lived are found to have functioned as primary controls on the

complex preservation of *Funisia*. However, the occurrence of *Funisia* in both cluster-type and surface-type assemblages of similar abundance in the ORS and PLRUS facies suggest that in life, the energy regimes had little impact on populations of *Funisia*. The ability of *Funisia* to dominate ecosystems in environments of variable energy levels is suggestive of an exceptional adaptability of *Funisia.* In future work, determining the origin of this suitability to a diversity of challenging environments, for instance whether it can be attributed to phylogenetic advantage or the popular tubular morphology, will help in understanding the tubular morphotype as a whole and its variable function within Ediacaran ecosystems.

REFERENCES

BOBROVSKIY, I., HOPE, J.M., IVANTSOV, A., NETTERSHEIM, B.J., HALLMANN, C., and BROCKS, J. J., 2018, Ancient steroids establish the Ediacaran fossil *Dickinsonia* as one of the earliest animals: Science, v. 361, p. 1246–1249, doi: 10.1126/science.aat7228.

CHEN, Z., BENGSTON, S., ZHOU, C.M., HUA, H., and YUE, Z., 2008, Tube structure and original composition of *Sinotubulites*: Shelly fossils from the late Neoproterozoic in southern Shaanxi, China: Lethaia, v. 41, p. 37–45, doi: 10.1111/j.1502-3931.2007.00040.x.

COHEN, P. A., BRADLEY, A., KNOLL, A.H., GROTZINGER, J.P., JENSEN, S., ABELSON, J., HAND, K., LOVE, G., METZ, J., MCLOUGHLIN, N., MEISTER, P., SHEPARD, R., TICE, M., and WILSON, J.P., 2009, Tubular compression fossils from the Ediacaran Nama Group, Namibia: Journal of Paleontology, v. 83, p. 110–122, doi: 10.1666/09-040R.1.

DROSER, M.L., GEHLING, J.G., and JENSEN, S.R., 2006, Assemblage palaeoecology of the Ediacara biota: The unabridged edition?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 232, p. 131–147, doi: 10.1016/j.palaeo.2005.12.015.

DROSER, M.L. and GEHLING, J.G., 2008, Synchronous aggregate growth in an abundant new Ediacaran tubular organism: Science, v. 319, p. 1660–1662, doi: 10.1126/science.1152595.

DROSER, M.L. and GEHLING, J.G., 2015, The advent of animals: The view from the Ediacaran: PNAS. v. 112, p. 4865–4870, doi: 10.1073/pnas.1403669112.

DROSER, M.L., TARHAN, L.G., and GEHLING, J.G., 2017, The rise of animals in a changing environment: global ecological innovation in the late Ediacaran: Annual Review of Earth and Planetary Sciences, v. 45, p. 593–617, doi: 10.1146/annurev-earth-063016-015645.

DROSER, M.L., GEHLING, J.G., TARHAN, L.G., EVANS, S.D., HALL, C.M.S., HUGHES, I.V., HUGHES, E.B., DZAUGIS, M.E., DZAUGIS, M.P., DZAUGIS, P.W., and RICE, D., 2019, Piecing together the puzzle of the Ediacara biota: Excavation and reconstruction at the Ediacara National Heritage Site Nilpena (South Australia): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 513, p. 132–145, doi: 10.1016/j.palaeo.2017.09.007.

EVANS, S.D., DROSER, M.L., and GEHLING, J.G., 2015, *Dickinsonia* liftoff: Evidence of current derived morphologies: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 434, p. 28–33, doi: 10.1016/j.palaeo.2015.02.006.

EVANS, S.D., DROSER, M.L., and GEHLING, J.G., 2017, Highly regulated growth and development of the Ediacara macrofossil *Dickinsonia costata*: PLOS ONE, v. 12, e0176874., doi: 10.1371/journal.pone.0176874.

EVANS, S.D., GEHLING, J.G., and DROSER, M.L., 2019a, Slime travelers: Early evidence of animal mobility and feeding in an organic mat world: Geobiology, v. 00, p. 1–20. doi: 10.1111/gbi.12351.

EVANS, S.D., HUANG, W., GEHLING, J.G., KISAILUS, D., and DROSER, M.L., 2019b, Stretched, mangled, and torn: Responses of the Ediacaran fossil *Dickinsonia* to variable forces: Geology, v. 47, p. 1049–1053, doi: 10.1130/G46574.1.

FEDONKIN, M.A. and WAGGONER, B.M., 1997, The late Precambrian fossil *Kimberella* is a mollusk-like bilaterian organism: Nature, v. 388, p. 868–871, doi: 10.1038/42242.

FINNEGAN, S., GEHLING, J.G., and DROSER, M.L., 2019, Unusually variable paleocommunity composition in the oldest metazoan fossil assemblages: Paleobiology, v. 45, p. 235–45, doi: 10.1017/pab.2019.1.

GEHLING, J.G., 1999, Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks: PALAIOS, v. 14, p. 40–57, doi: 10.2307/3515360.

GEHLING, J.G., 2000, Environmental interpretation and a sequence stratigraphic framework for the terminal Proterozoic Ediacara Member within the Rawnsley Quartzite, South Australia: Precambrian Research, v. 100, p. 65–95, doi: 10.1016/S0301-9268(99)00069-8.

GEHLING, J.G., and DROSER, M.L., 2009, Textured organic surfaces associated with the Ediacara biota in South Australia: Earth-Science Reviews, v. 96, p. 196–206, doi: 10.1016/j.earscirev.2009.03.002.

GEHLING, J.G., and DROSER, M.L., 2013, How well do fossil assemblages of the Ediacara biota tell time?: Geology, v. 41, p. 447–450, doi: 10.1130/G33881.1.

HALL, C.M.S., DROSER, M.L., GEHLING, J.G., and DZAUGIS, M.E., 2015, Paleoecology of the enigmatic *Tribrachidium*: New data from the Ediacaran of South Australia: Precambrian Research, v. 269, p. 183–194, doi: 10.1016/j.precamres.2015.08.009.

HARTIGAN, J.A., and HARTIGAN, P.M., 1985, The dip test of unimodality: The Annals of Statistics, v. 13, p. 70-84.

JENSEN, S., DROSER, M.L., and GEHLING, J.G., 2006, A critical look at the Ediacaran trace fossil record, *in* Xiao, S. and Kaufman, A.J. (eds.), Neoproterozoic Geobiology and Paleobiology: Springer Netherlands, Dordrecht, p. 115–157, doi: 10.1007/1-4020-5202-2_5.

JOEL, L.V., DROSER, M.L., and GEHLING, J.G., 2014, A new enigmatic, tubular organism from the Ediacara Member, Rawnsley Quartzite, South Australia: Journal of Paleontology, v. 88, p. 253–262, doi: 10.1666/13-058.

LEWIN, R., 1984, Alien beings here on Earth: Science, v. 223, p. 39.

LIU, A.G., KENCHINGTON, C.G., and MITCHELL, E.G., 2015, Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota: Gondwana Research, v. 27, p. 1355-1380, doi: 10.1016/j.gr.2014.11.002.

MACGABHANN, B.A., J.D. SCHIFFBAUER, J.W. HAGADORN, P.V. ROY, E.P. LYNCH, L. MORRISON, J. MURRAY, 2019, Resolution of the earliest metazoan record: Differential taphonomy of Ediacaran and Paleozoic fossil molds and casts: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 513, p. 146–165, doi: 10.1016/j.palaeo.2018.11.009.

MARSHALL, D., 1996, Ternplot: An excel spreadsheet for ternary diagrams: Computers and Geosciences, v. 22, p. 697–699, doi: 10.1016/0098-3004(96)00012-X.

MITCHELL, E.G., KENCHINGTON, C.G., LIU, A.G., MATTHEWS, J.J., and BUTTERFIELD, N.J., 2015, Reconstructing the reproductive mode of an Ediacaran macro-organism: Nature, v. 524, p. 343–346, doi: 10.1038/nature14646.

SAPPENFIELD, A., DROSER, M.L., and GEHLING, J.G., 2011, Problematica, trace fossils, and tubes within the Ediacara Member (South Australia): Redefining the Ediacaran trace fossil record one tube at a time: Journal of Paleontology, v. 85, p. 256–265, doi: 10.1666/10-068.1.

SCHIFFBAUER, J.D., HUNTLEY, J.W., O'NEIL, G.R., DARROCH, S.A.F., LAFLAMME, M., and CAI, Y., 2016, The latest Ediacaran wormworld fauna: Setting the ecological stage for the Cambrian explosion: GSA Today, v. 26, p. 4–11, doi: 10.1130/GSATG265A.1.

TARHAN, L.G., DROSER, M.L., and GEHLING, J.G., 2010, Taphonomic controls on Ediacaran diversity: Uncovering the holdfast origin of morphologically variable enigmatic structures: PALAIOS, v. 25, p. 823–830, doi: 10.2110/palo.2010.p10-074r.

TARHAN, L.G., DROSER, M.L., GEHLING, J.G., and DZAUGIS, M.P., 2015, Taphonomy and morphology of the Ediacara form genus *Aspidella*: Precambrian Research, v. 257, p. 124–136, doi: 10.1016/j.precamres.2014.11.026.

TARHAN, L.G., HOOD, A.V.S., DROSER, M.L., GEHLING, J.G., and BRIGGS, D.E.G., 2016, Exceptional preservation of soft-bodied Ediacara biota promoted by silica-rich oceans: Geology, v. 44, p. 951–954, doi: 10.1130/G38542.1.

TARHAN, L.G., DROSER, M.L., GEHLING, J.G., and DZAUGIS, M.P., 2017, Microbial mat sandwiches and other anactualistic sedimentary features of the Ediacara Member (Rawnsley Quartzite, South Australia): Implications for interpretation of the Ediacaran sedimentary record: PALAIOS, v. 32, p. 181–194, doi: 10.2110/palo.2016.060.

TARHAN, L.G., DROSER, M.L., COLE, D.B., and GEHLING, J.G., 2018, Ecological expansion and extinction in the Late Ediacaran: Weighing the evidence for environmental and biotic drivers: Integrative and Comparative Biology, v. 58, p. 688–702, doi: 10.1093/icb/icy020.

WADE, M., 1968, Preservation of soft-bodied animals in Precambrian sandstones at Ediacara, South Australia: Lethaia, v. 1, p. 238–267, doi: 10.1111/j.1502-3931.1968.tb01740.x.