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Ecology and Biology of *Dickinsonia*, an Iconic Member of the Ediacara Biota From
Nilpena, South Australia

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

Geological Sciences

by

Scott Daniel Evans

June 2015

Thesis Committee:
    Dr. Mary L. Droser, Chairperson
    Dr. Nigel C. Hughes
    Dr. Richard A. Minnich

The Thesis of Scott Daniel Evans is approved:

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_____

Committee Chairperson

University of California, Riverside

Acknowledgements

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Chapter 1

Abstract

Dickinsonia, an iconic member of the Ediacara biota, is abundant in the Ediacaran deposits found at the Nilpena field site, South Australia. Despite exquisite fossil preservation at this site, many specimens of *Dickinsonia* appear to be incomplete, with an apparently "missing piece" on the periphery. Orientation measurements from specimens on three fossil beds suggest that these so-called "missing pieces" are aligned irrespective of the axial orientation of *Dickinsonia*. The nonrandom orientation of incomplete specimens matches that of other aligned structures found on two of these beds. The preferred directionality of this feature suggests the molding of incomplete specimens under the influence of current activity prior to or during burial. We propose that this feature originates where part of a *Dickinsonia* was lifted off of the substrate during a storm event and that sand was deposited beneath this lifted portion. This model suggests that *Dickinsonia* was easily separated from the sea floor and was not attached to the substrate on which it lived. This is consistent with the data from *Dickinsonia* footprints suggesting that *Dickinsonia* was mobile.

Introduction

Fossils of the Ediacara biota represent the earliest evidence of macroscopic, complex organisms on Earth. This diverse assemblage of soft-bodied organisms helps to bridge the evolutionary gap between microscopic, unicellular life forms present through most of Earth's early history and complex, familiar modern forms.

The Ediacara Member of the Rawnsley Quartzite crops out in the Flinders Ranges area of South Australia (Fig. 1). The fossilized biota of the Ediacara Member consists of a morphologically diverse array of organisms preserved as molds and casts belonging to the White Sea assemblage, named for similar remains found in Russia (Narbonne, 2005).

Dickinsonia is one of the most abundant and recognizable taxa preserved in the Ediacara Member of South Australia. Proposed biologic affinities for this soft-bodied taxon range widely from annelids (Wade, 1972), to fungi or lichens (Retallack, 2007), to protists (Seilacher et al., 2003), to an extinct animal kingdom (Seilacher, 1992), and most recently to the extant animal phylum Placozoa (Sperling and Vinther, 2010). Attempts at determining the biologic affinity of *Dickinsonia*, and many other members of the Ediacara biota, have yielded largely inconclusive results. An alternative approach is to examine paleoecological and taphonomic attributes to constrain their ecology and biology without the limitations of attempting to place them into known phylogenetic classifications. Here we report a taphonomic peculiarity of *Dickinsonia* observed in numerous specimens from the Ediacara Member of South Australia in that many specimens exhibit a unique morphology in which part of the organism appears to be missing (Fig. 2).
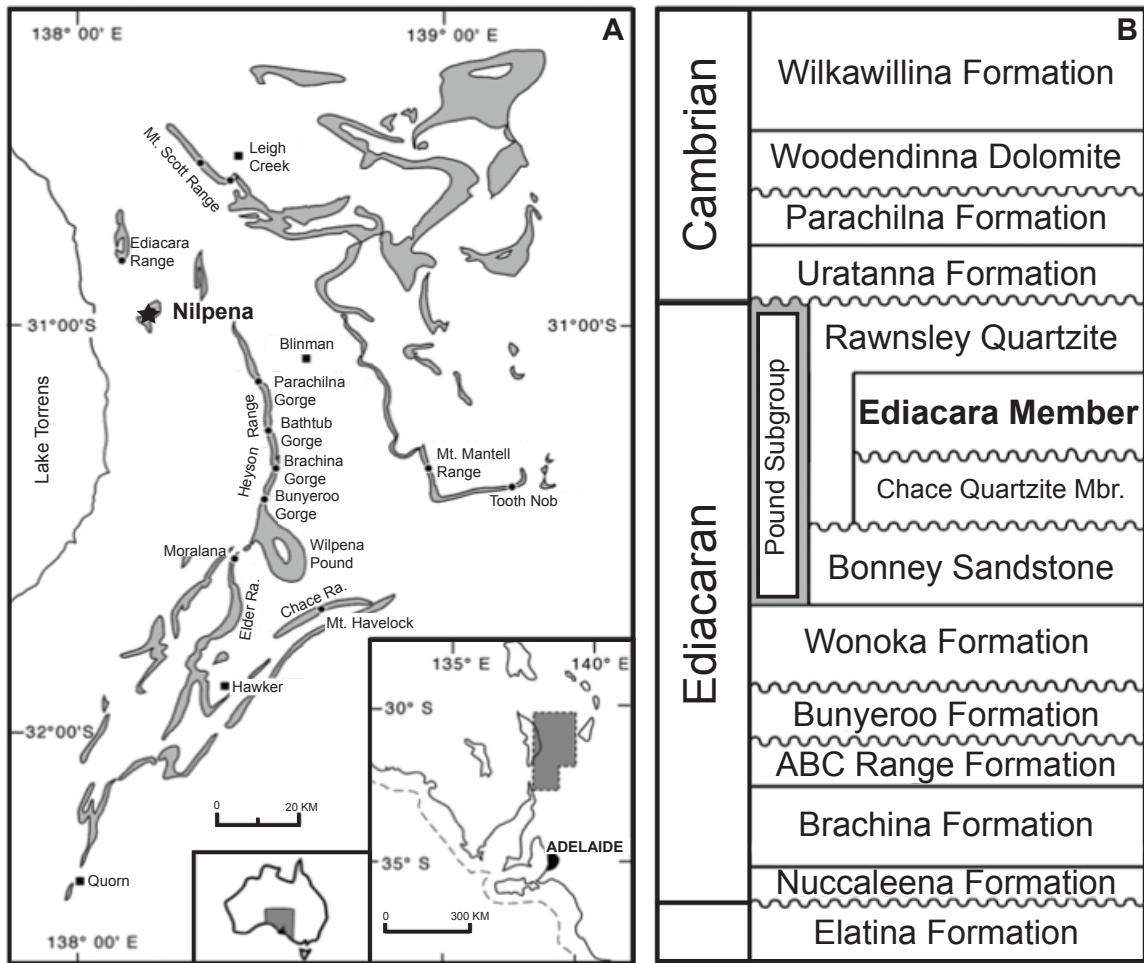
Fure 1. a) Map of the Flinders Ranges showing the Nilpena field locality, marked with the black star; and b) Stratigraphic section showing the position of the Ediacara Member in bold (edited from Gehling and Droser, 2009).

Geologic Setting, Preservation and Sampling Methods

On the western side of the Flinders Ranges in South Australia, at the National Heritage Nilpena Ediacara fossil site, the Ediacara Member fills a surface with relief of 10-300 m cut into the underlying Chace Quartzite Member of the Rawnsley Quartzite and occurs 200-600 m below a basal Cambrian disconformity (Fig. 1; Gehling, 2000). The Ediacara Member consists of five facies, with *Dickinsonia* occurring most commonly in

the Wave-base Sand facies of Gehling and Droser (2013) characterized by thinly bedded, rippled quartz sandstones deposited between fair-weather and storm wave-base. Preservation of benthic communities of the Ediacara biota, on organic mat-bound substrates, was by episodic storm surge and flows (Gehling, 2000).

Fossils of the Wave-based Sand facies occur as casts and molds on the bases of sandstone beds. Identical counterpart casts and molds of fossils also exist on the tops of underlying beds, but are rarely preserved because these are generally thinly laminated, discontinuous sand layers. These layers filled wave ripple troughs after storm events, and were subsequently colonized by microbial mats and benthic megascopic organisms of the Ediacara biota in the hiatuses between storm events. As a consequence, field study is largely confined to the thicker bedded event sands that smothered and molded the upper surfaces of more resilient organisms or cast the collapsed bodies, or pedal-imprints, of the less resilient organisms (Gehling, 1999). The sole surfaces of these event beds are generally cleanly separated from the underlying sands due to early cementation of a "sole veneer" that effectively produced a pyritized "death mask" of the substrate including the topology of all organisms involved. In the White Sea region of NW Russia pyrite is still preserved (Fedonkin, 2003). In the deeply weathered outcrops of South Australia, all that remains is a hematitic rind on the sole surface. In the relatively coarse grained and deeply weathered strata at Nilpena, much of the iron has long been leached out.

Specimens of *Dickinsonia* and other organisms were preserved when overlying sand cast the top of the organism (Gehling, 1999). This process results in fossils of

Dickinsonia preserved as negative impressions on the bases of fossil beds. Counter-parts of these casts occur on bed tops with less regularity.

Because the fossils are preserved on the base of beds, fossiliferous beds must be systematically flipped and pieced back together. Such work at the Nilpena field site has been ongoing for the past twelve years and has resulted in the excavation of 28 fossil bearing beds, yielding over 300 m^2 of *in situ* material and more than 400 *Dickinsonia*. Three beds, bed MM3, STCI, and STCH, contain *Dickinsonia* exhibiting a unique morphology, with 34 percent of all specimens on these beds appearing to be incomplete. Orientation measurements for specimens themselves were taken on bed MM3 by determining the angle of the intersection between true north of the midline of the specimen. The orientation of these "missing pieces" was recorded for all beds measuring the angle in degrees north of an imaginary line from the missing feature to the center of the specimen. Orientation data was also collected for other structures that are aligned on beds MM3 and STCH. Specimens were also digitally photographed and molded in latex to allow corroboration with field data. Rose diagrams for both specimen and missing piece were compiled using PAST software (Hammer et al., 2001).
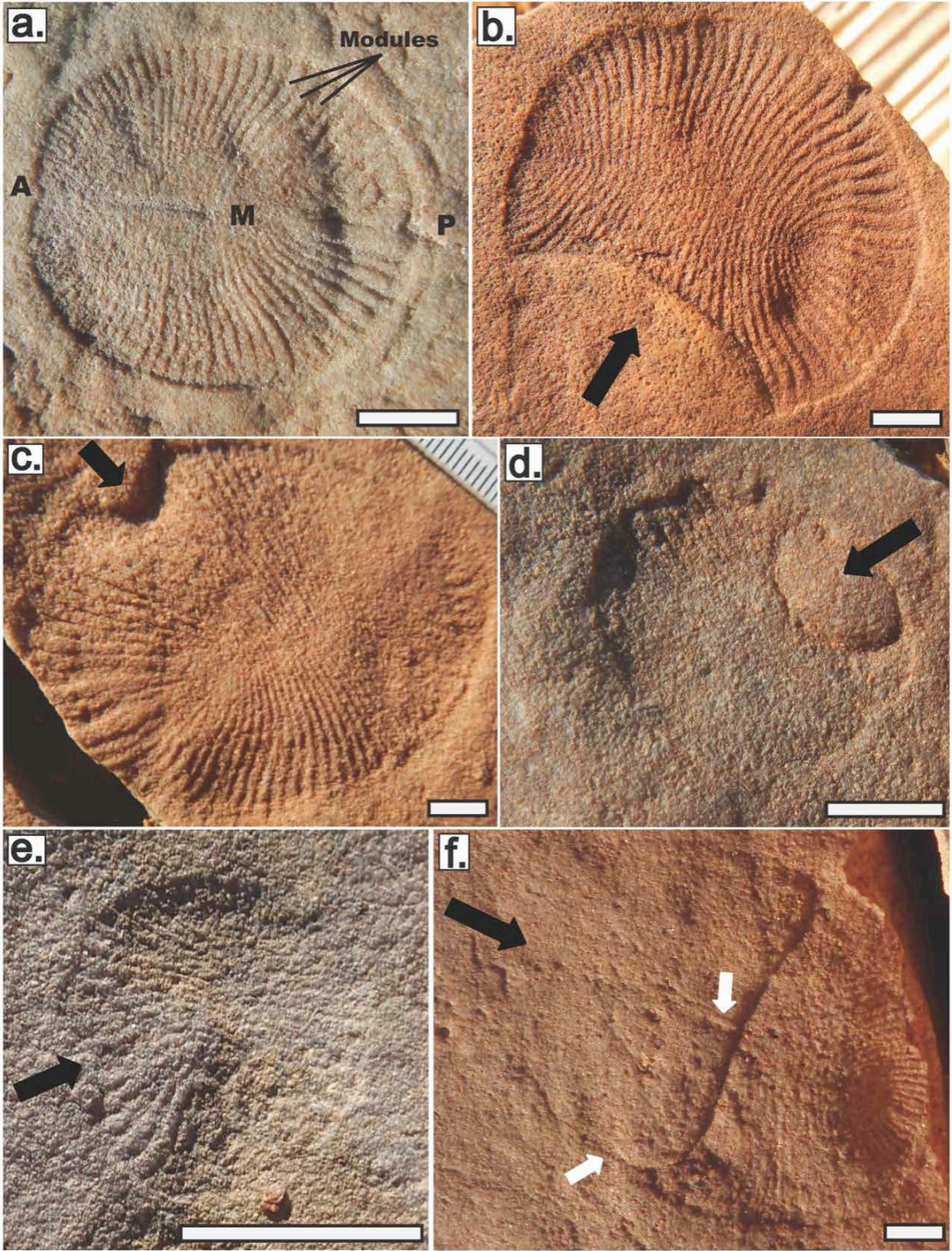
Figure 2. Fossil specimens of Dickinsonia from the Ediacara Member, Rawnsley Quartzite. a) The classic morphology of a well preserved specimen showing the posterior (P), anterior (A), midline (M), and the modules. (a) 1TFB-01. b–f) Specimens exhibiting the varying missing piece morphologies with missing pieces indicated by black arrows and ghost impressions left underneath the lifted portions indicated by white arrows. (b) SAM specimen P49420. (c) MMB3-01. (d) MMB3-02. (e) STCI-01. (f) Bed STCH-01. All scale bars = 5 cm.

Dickinsonia

Dickinsonia is well known from deposits of the White Sea region of Russia and the Ediacaran Hills of South Australia (Narbonne, 2005). There are currently five recognized species of *Dickinsonia*, making it unusual amongst these taxa as a fossil genus with multiple known species (Gehling et al., 2005). The morphology of *Dickinsonia* varies between species but can be generally described as ovoid in shape with a midline along the long axis (Fig. 2a). *Dickinsonia* is divided into modules that tapper at the anterior end. These features resemble segments but the extent of the division between each module, and thus its relation to segmentation seen in many modern organisms such as annelids or arthropods, is not known (Sperling and Vinther, 2010).

Dickinsonia is characterized by a range of preservational modes, including folded and ripped individuals, suggesting that this organism was durable in spite of being soft-bodied. Flume expirements and reconstructions of this organism as a fungi or lichen have called into question the interpretation that *Dickinsonia* was a free-living organism (Schopf and Baumiller, 1998; Retallack, 2007). However, trace fossil evidence also suggests that *Dickinsonia* was capable of movement (Gehling et al., 2005; Sperling and Vinther, 2010). Trace fossils of *Dickinsonia* are viewed as positive features on bed soles referred to as "footprints" (Gehling et al., 2005). These footprints are commonly found as a set of two or more that rarely have a *Dickinsonia* of similar size at the end of this "track-way" (Gehling et al., 2005; Sperling and Vinther, 2010). The close proximity of identically sized *Dickinsonia* with footprints indicates that they represent depressions left on the sea floor when the *Dickinsonia* remained in one place for an extended period of

time (Sperling and Vinther, 2010). These depressions are then filled with the overlying sand and are preserved as positive features on the bases of beds. Where preservation is exceptional segmentation patterns from the bottom of the *Dickinsonia* may occur in footprints.

Missing Pieces

Over 80 *Dickinsonia* specimens are incompletely preserved (Fig. 2b). Specimens can be otherwise well preserved but appear to have a missing piece. This characteristic ranges from extremely small missing portions (Fig. 2c, e) to examples were approximately half of the organism appears to be absent (Fig. 2f). The missing fragment is expressed in various forms, from round, half circle shaped pieces (Fig. 2b, d, e) to v-shaped pieces that appear to have been cleanly cut from the organism (Fig. 2c). Despite this morphological variation all specimens identified as incomplete show a smooth re-entrant or straight margin in association with missing portions (Fig. 2). In some specimens a faint, ghost like ring appears to outline the incomplete area of the *Dickinsonia* (Fig. 2f). This ring is similar to the footprint feature described above and rarely faint segmentation occurs in this 'ghost' region. Missing pieces do not form preferentially on any portion of the *Dickinsonia* with respect to the midline, the assumed posterior or anterior end.

Orientation of the Missing Piece on Fossil Beds

Bed MM3 is approximately 25 m^2 and contains 189 *Dickinsonia* specimens. Orientation measurement of 153 specimens (orientation measurements are not possible when segmentation is not present) shows no systematic alignment of *Dickinsonia* (Fig.

3a). Of the *Dickinsonia* on bed MM3, 69 are not complete specimens as described above.

Orientation measurement of missing portions reveals a nonrandom alignment (Fig. 3b).

Bed STCI, 16 m^2, contains 38 total *Dickinsonia*, seven of which clearly exhibit this

feature. Despite a low sample size these missing pieces also appear to be nonrandomly

aligned on bed STCI (Fig. 3d). Bed STCH, 12 m^2, also has a low number of total

Dickinsonia with only ten specimens, four of which seem to be incomplete. Again on

STCH this incomplete feature demonstrates preferential orientation (Fig. 3e).

Other Aligned Features

        Both Beds MM3 and STCH contain additionally aligned biogenic structures. Bed

MM3 contains 43 specimens of the biogenic structure mop. Mop is interpreted as a

pullout structure that forms when holdfasts of frond organisms are ripped out of the

organic mat bound substrate on which they existed (Tarhan et al., 2010). This removal

disturbs the organic mat surface and leaves behind biogenic structures that have been

demonstrated to be strongly current aligned (Tarhan et al., 2010). The Mop alignment

(Fig. 3c) is consistent with that found for *Dickinsonia* missing pieces from the same bed

(Fig. 3b). Bed STCH includes toppled fronds that are preserved with their holdfasts (Fig.

4). Despite low specimen numbers, these felled organisms are also strongly aligned (Fig.

3f). Again, the alignment of the missing pieces of *Dickinsonia* and that found for these

fronds are parallel (Fig. 3e, f).
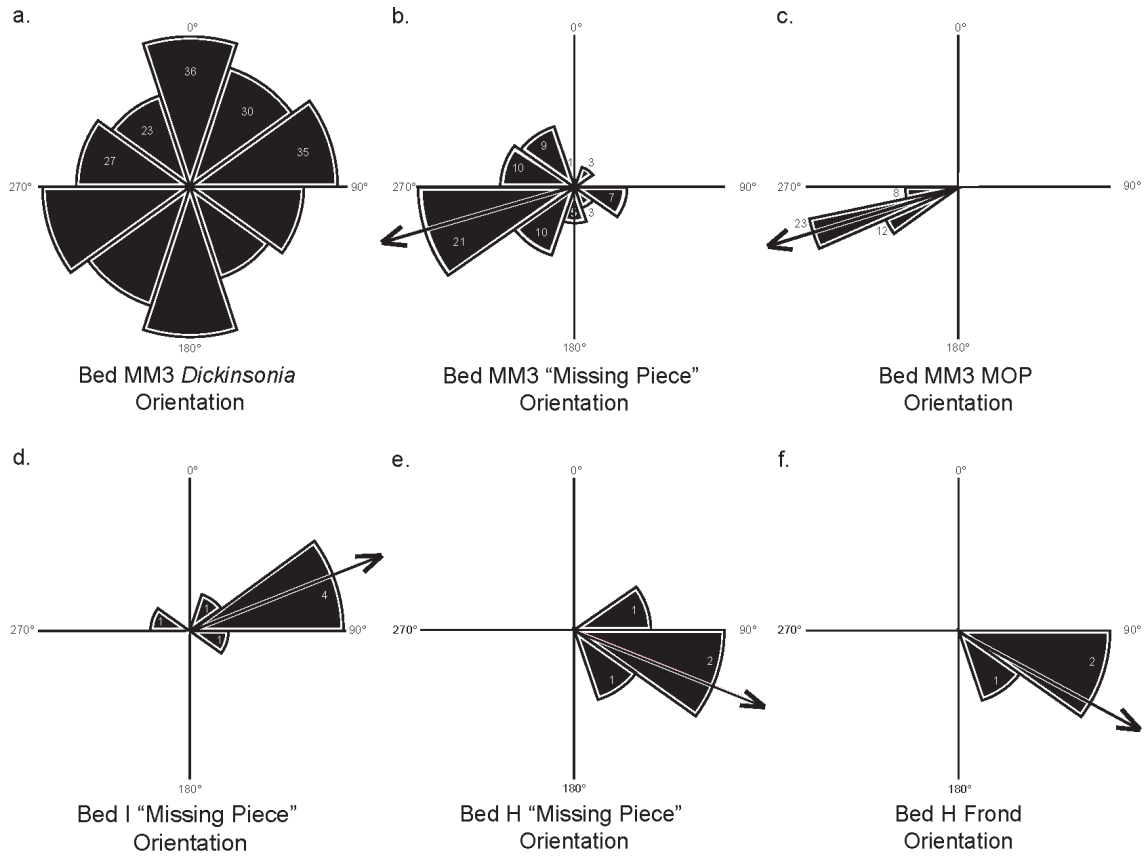
Figure 3. Rose diagrams for orientations of; a) Dickinsonia main body axis from bed MM3; b) missing pieces of Dickinsonia from bed MM3; c) mop specimens from bed MM3; d) missing pieces of Dickinsonia from bed STCI; e) missing pieces of Dickinsonia from bed STCH; and f) toppled fronds from bed STCH.

Figure 4. Toppled fronds from Bed H outlined in chalk with arrow indicating current direction.

Discussion

The alignment of the missing pieces of *Dickinsonia* suggests that the formation of this feature was somehow influenced by current flow. The nonrandom orientation of any fossil structure in a marine setting is almost exclusively attributed to current activity (Nagel, 1967; Kidwell et al., 1986). The alignment of mop and fronds also suggests that current activity impacted these beds. The presence of fronds and holdfast on Bed STCH allows the determination of alignment because we can identify where the organism was

anchored to the substrate and therefore the current direction that must have felled the specimen. The agreements in purposed current direction between *Dickinsonia* and mop on bed MM3 and fronds on Bed STCH further supports the idea that this feature formed in the presence of current action.

Our evidence reveals that incompletely preserved *Dickinsonia* specimens are not a result of the systematic loss of pieces of the specimens but rather that part of the organism was lifted off of the sea floor during burial and thus, the full body morphology is not preserved. We suggest that *Dickinsonia* was a free-living organism that was not attached to the substrate, and that under 'normal' conditions lay with its entire underside in contact with the seafloor (Fig. 5a). This 'normal' life-position would have been disrupted during storm events as associated currents lifted part of the *Dickinsonia* off of the seafloor (Fig. 5b) allowing the transported sediment to accumulate beneath the lifted portion of the specimen (Fig. 5c). The deposition of sand below part of the organism would have resulted in a gap between the lifted portion of the *Dickinsonia* and the organic mat surface. This biological surface is integral to the "death mask" style of preservation outlined above and thus, this separation would lead to the lack of preservation of the lifted portion. This lifted fragment then appears to be 'missing' because it is not present on the excavated bed surface.

Life Position
a.

Storm Event
b.
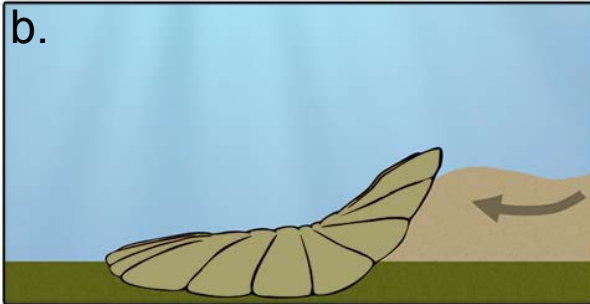
Burial
c.
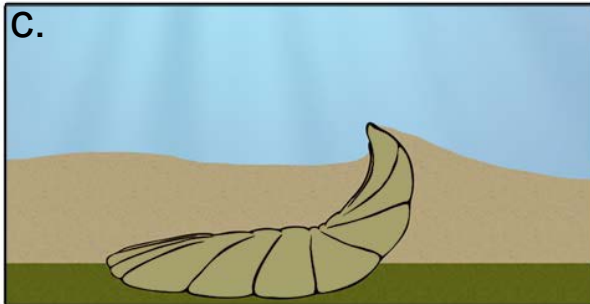
Figure 5. Cross sectional reconstruction of the formation of the missing piece of Dickinsonia showing: a) Dickinsonia in life position with the entirety of the underside in contact with the mat-bound substrate; b) the lifting of part of the specimen during a current event associated with the transport and/or deposition of sediment; and c) the deposition of sediment resulting in separation between the lifted portion of the Dickinsonia and the organic mat surface that results in the formation of an apparent missing piece. Reconstruction by Michelle Kroll.

The ghost rings rarely outlining the missing portions of *Dickinsonia* also support this model. Faint rings and associated positive features represent footprint like scenarios where the impression left by a resting *Dickinsonia* is filled with sand in the area below the lifted portion. Faint segmentation may also occur when the *Dickinsonia* is only slightly lifted off of the seafloor and the bottom of the lifted portion is still visible on the bedding plane.

The model described above offers new insights that further our understanding of *Dickinsonia*. The fact that *Dickinsonia* could be easily lifted off of the sea floor suggests that it was a free-living organism and not directly attached to the substrate. This is consistent with the hypothesis that *Dickinsonia* was capable of movement, as has been suggested by many previous authors (Ivantsov and Malakhovskaye, 2002; Gehling et al., 2005; Sperling and Vinther, 2010). This strongly questions the interpretation of Retallack (1994) that *Dickinsonia* was a fungi or lichen. Modern fungi and lichen are attached to the substrate on which they live. If *Dickinsonia* were glued in this fashion to the Ediacaran sea floor any missing fragment would have to be ripped or torn from the sea floor as well as the rest of the organism that remained attached. The smooth nature of all margins associated with the missing features and ghost imprints described above suggests that these fragments have not been ripped from the main body but rather remained attached and instead are simply not viewed in the plane of bedding. This result also eliminates some of the hypotheses proposed by Schopf and Baumiller (1998) who concluded that *Dickinsonia* could not have withstood current activity typical of this environment if constructed as an annelid worm without it having been attached. The

lifting of specimens suggests that either *Dickinsonia* was much more dense than their model predicts or that the nature of the organic mat lining the seafloor during this time increased friction between the specimen and the substrate holding the organism in place. It is also possible that the footprints left by *Dickinsonia* indicate that it was somehow imbedded in the organic substrate and was therefore more resistant to current flow than if it were simply resting on top of a sandy surface. Our interpretation that part of the organism could be lifted off of the mat presents a view of *Dickinsonia* as an entity distinctly separate from the substrate on which it lived.

Conclusions

Incomplete specimens of *Dickinsonia* on three beds from the Nilpena site reflect alignment of lifted sections during storm activity. High energy events lifted a portion of the organism off of the sea floor and deposited sand beneath it. This resulted in the partial preservation of these lifted specimens. The smooth nature of the margin around the lifted portion suggests that these features are not the result of detaching a piece of this organism from the preserved body. This indicates that *Dickinsonia* was a free-living, non-attached organism and supports other evidence that it may have been capable of some form of movement.

Chapter 2

Abstract

Dickinsonia costata, the iconic Ediacaran fossil of South Australia, occurs abundantly in the Ediacara Member of the Rawnsley Quartzite cropping out in the Flinders Ranges, South Australia. Examination of specimens from the Nilpena Field Site demonstrates that *D. costata* ranges in length from 3.6 mm to 167.4 mm and occurs in varying abundance within and across facies. Abundance data normalized to exposed surface area show that this organism preferred a relatively shallow water, fair-weather wave base habitat. Within this setting *D. costata* exhibits variable density of occurance and size distributions. The substrate dominated by fossils of *Aspidella* and *Funisia* limited the presence of *D. costata*. Ubiquitous *Funisia* in the absence of *Aspidella* was limiting with respect to size, preserving larger populations of *D. costata*, while juvenile forms occur preferentially in an inferred algal-dominated seafloor. Based on evidence from organic mat coverings, the timing of depositional events controlled the maximum size ranges of *D. costata*, with small populations representing communities buried before they fully developed. The biology of *D. costata* is reflected in the overall right-skewed, log-normal size frequency curve, demonstrating a pattern of high infant mortality. Individual populations exhibit varying size frequency distributions. A single bed contains more than half of the *D. costata* at Nilpena and the absence of cohorts within this large population is suggestive of continuous recruitment.

Introduction

The enigmatic members of the Ediacara biota represent the earliest known examples of morphologically complex, community forming organisms. While stem group metazoans were most likely extant during the Ediacaran, determining the biological affinities for specific taxa remains difficult (Gehling et al., 2005; Xiao and Laflamme, 2008; Erwin et al., 2011). Recent studies have focused on specific biologic and ecological attributes of Ediacara organisms.

Dickinsonia is an iconic fossil of the Ediacara biota found in South Australia and Russia. There are currently five recognized species of *Dickinsonia* and the most common species of this genus at the Nilpena field site, South Australia, is *D. costata*. This species is ovoid in shape and is divided into modules (segment-like structures) that taper and are presumably inserted at the posterior end (Fig. 2a). *Dickinsonia* was one of the first macroscopic organisms capable of intermittent movement, as evident by traces preserved in positive hyporelief that are inferred to represent areas where the organism remained stationary for some period of time (Gehling et al., 2005). The timing, extent and mechanism for locomotion remain unresolved (Gehling et al., 2005, Sperling and Vinther, 2010). Specimens varying widely in morphology indicate that *Dickinsonia* was durable for a soft-bodied organism and experienced multiple forms of deformation, but the composition of the organism is unknown. Phylogenetic interpretations of *Dickinsonia* vary greatly from it being an annelid (Wade, 1972), a fungi or lichen (Retallack, 2007), a protist (Sielacher et al., 2003), belonging to the extinct kingdom Vendobionta (Sielacher, 1992), and recently as a member of the extant phylum Placozoa (Sperling and Vinther,

2010). These classifications are subject to varying levels of scrutiny and, while classifications such as annelids, fungi and lichen can be definitively rejected, no biologic affinity has been convincingly determined for *Dickinsonia*.

The Ediacara Member of the Rawnsley Quartzite cropping out in the Flinders Ranges in South Australia (Fig. 1a) contains abundant and morphologically diverse fossilized organisms. The most common fossils are considered part of the White Sea assemblage, named for Russian deposits with similar fauna. Examination of several disparate facies within the Ediacara Member has demonstrated that three classic assemblages, the White Sea, Avalon, and Nama, of the Ediacara biota are present (Narbonne, 2005; Gehling and Droser, 2013). Excavated bedding planes of the Ediacara Member at a field site west of the Flinders Ranges allow the examination of *in situ* fossil communities (Fig. 6). The exquisite preservation at this site provides an unparalleled opportunity to examine the paleobiology and paleoecology of these organisms within individual populations.

Dickinsonia occurs in all fossil-bearing facies and is one of the most common fossils in the Ediacara Member. Here we examine the nature of populations with respect to abundance, density and size and test possible controls on the distribution of *Dickinsonia*.
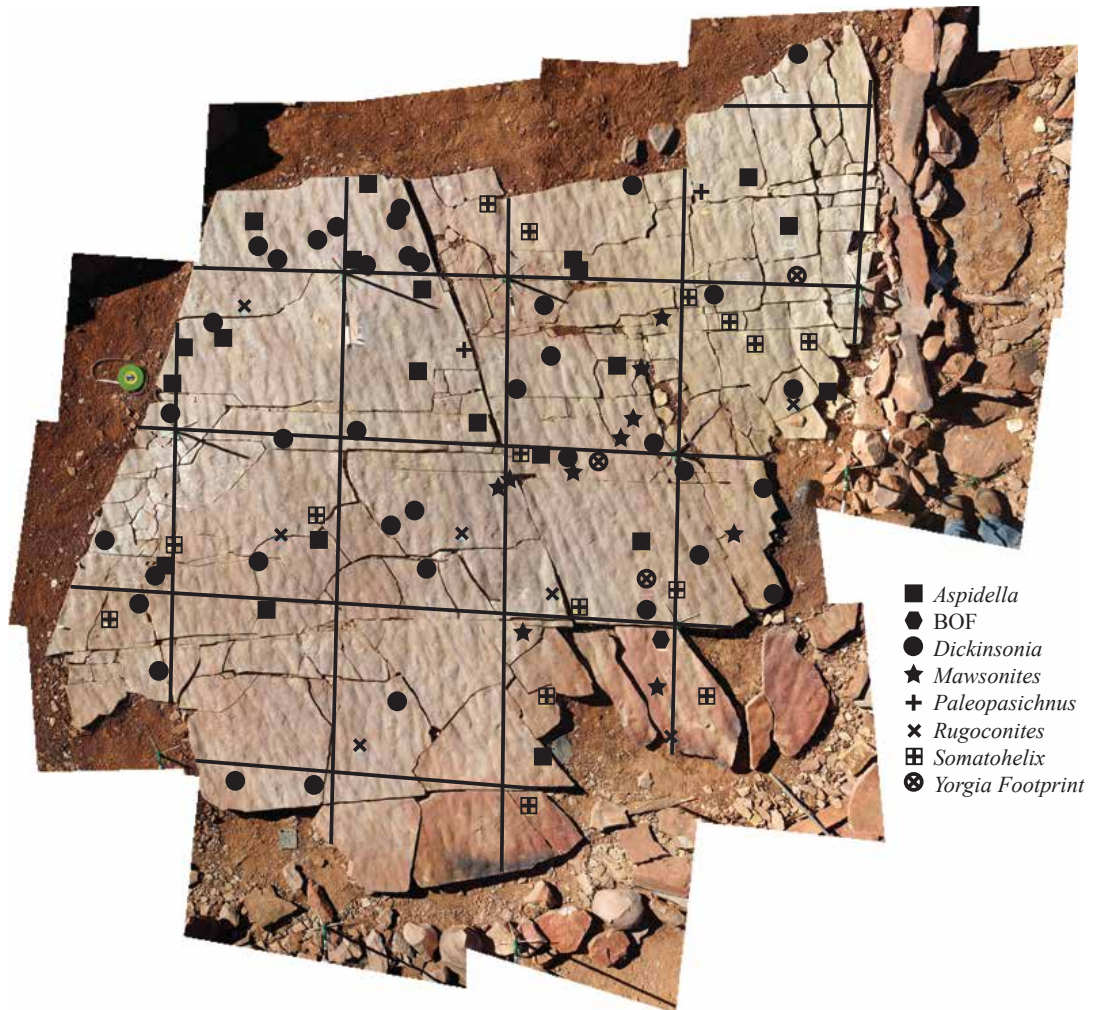
Figure 6. Composite photograph of bed STCI from Nilpena South Australia with fossil specimens indicated by symbols. Grids represent meter-by-meter squares.

Geologic Setting

The Rawnsley Quartzite is divided into two members, the Ediacara Member and the Chace Quartzite Member (Fig. 1b). The Ediacara Member ranges in thickness from 10-300 m and is preserved 200-600 m below a basal Cambrian disconformity (Gehling, 2000). The Nilpena field site, located west of the Flinders Ranges, South Australia, contains outcrops representative of five fossiliferous facies: the Shoreface Sands, Wave-Base Sands, Delta-Front Sands, Sheet-Flow Sands and Mass-Flow Sands. Each facies represents a distinct environment with varying levels of water depth and energy (Gehling and Droser, 2013). Fossils are typically preserved on the bases of beds, necessitating the excavation and systematic overturning of these surfaces. Over the last thirteen years such work at Nilpena has resulted in the exhumation of 28 beds and over 300 m^2 of *in situ* fossiliferous material from the Wave-Base Sands facies and the Sheet-Flow Sands facies (see Joel et al., 2015). This unique preservation and bed excavation allows the examination of distinct populations of Ediacaran organisms that lived contemporaneously.

Preservation of the Ediacara biota at Nilpena occurs in sandstone beds characterized by episodic deposition. The "death mask" model suggests that these fossils formed due to early mineralization by pyrite following burial (Gehling, 1999). Textured Organic Surfaces (TOS) are common on both fossiliferous and unfossiliferous beds in the Ediacara Member, which indicates the ubiquitous presence of microbial mats covering the seafloor during this time (Gehling and Droser, 2009). The storm deposition associated with the preservation of these fossils results in the most well preserved specimens

occurring on the bases of beds in both positive and negative hyporelief. Associated counterparts are occasionally preserved on bed tops. *Dickinsonia* body fossils occur in negative hyporelief on the bases of these beds, indicating that this organism did not collapse after burial in contrast to fossils that occur in positive hyporelief, such as the holdfast form genus *Aspidella*. Inferred resting traces of *Dickinsonia* are found in positive relief and are thought to be impressions left in the mat surface (Gehling et al., 2005; Droser and Gehling, 2014).

The Wave-Base Sand facies (WBSf) contains the most abundant and diverse fossil assemblages (Gehling and Droser, 2013). Rocks of this facies consist of wave-rippled, typically fine- to medium-grained sandstone beds, ranging in thickness from one mm to as much as 50-60 mm. At Nilpena there are currently three main sites, MM, STC and 1T, where successions of several beds from the WBSf have been excavated. The MM and STC sites are found within the same succession and likely within 2 m of each other stratigraphically (strata between these excavation sites are covered). The 1T site contains beds with finer grains relative to the other two sites. The ubiquitous wave-rippled sandstones represent deposition near wave-base. There are differences in substrate and physical energy between beds in this facies. For example, two relatively thick beds contain evidence of strong unidirectional currents, indicated by strongly oriented fronds and the presence of "mop", a biogenic structure that results from the extraction of holdfasts of frondose organisms from the substrate (Tarhan et al., 2010). Beds also differ in the extent of textured organic surfaces (TOS), with numerous beds containing evidence of a thick organic substrate and others with little evidence of mats.

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Methods

For a complete body size analysis we have compiled data from 959 specimens of *D. costata*, including those at the Nilpena field site (403 specimens) and others from the South Australia Museum (SAM, 556 specimens). Measurements of body size were taken from latex molds using digital calipers as length, measured along the midline, and width, measured perpendicular to the midline. Many specimens of *Dickinsonia* are incomplete, exacerbating the measurement of length and width. Sperling (personal comm.) have shown that *D. costata* has a nearly constant length to width ratio ($R^2 = 0.98$). Using their model we use incomplete specimens as long as we can obtain a width measurement to estimate length. This process results in 769 specimens of *D. costata* from which we can determine length at a ~2% accuracy. Given the consistency of the length to width ratio for *D. costata* we use maximum length to represent body size.

Fossil specimens on excavated surfaces are mapped to square meter grids assigned to each bed (Fig. 6). Surface area, abundance and density data as well as diversity and the percentage covered by TOS are then obtained from these bed maps. Statistical analyses for distributions were conducted using the PAST software (Hammer et al., 2001) and the MCLUST package in R (Farely and Raftery, 1999).

Statistical analysis was limited to the four beds with at least twenty *D. costata.* The Shapiro-Wilk test provides a statistical analysis of the normality of different distributions and was used on both logged and unlogged data sets (p-values > 0.05 indicating log-normal or normal distribution). We use Bayesian Information Criterion

(BIC) to analyze the likely number of size groupings for distributions of *D. costata* using

the MCLUST package in R (Fraley and Raftery, 2007). BIC provides a statistical

determination of whether 'clusters' observed in sfds represent individual cohorts or

whether the distribution is best represented by a single grouping, which have been

previously used to analyze reproductive strategies (Darroch et al., 2013; Zakrevskaya,

2015). MCLUST allows multivariate analysis to determine size groupings; here those

variables are the natural log of length and width. BIC favors less complex models by

adding penalties for each additional parameter, this is favored because less models with

fewer groupings are more likely to be biologically significant (Fraley and Raftery, 2007).

The most likely number of groupings is determined as that with the highest BIC value

with any difference greater than 10 considered statistically significant (Fraley and

Raftery, 1999). Using the MCLUST package for BIC analysis produces results from

multiple models, but we focus here on the four that allow unequal variance between

length and width, as they are the most likely to represent biologically realistic scenarios

and due to the consistent length to width ratio for *Dickinsonia.* These four models vary in

their assumptions of the volume, shape, and orientation of each size clustering (see Fraley

and Raftery, 1999, 2002, 2007). Because this method utilizes both length and width we

did not use any specimens for which we calculated length based on only width

measurements. Inconclusive results were interpreted based on BIC values not differing by

more than ten for multiple different numbers of size groupings and models.

Results

The length of *D. costata* ranges from 3.61 to 167.43 mm with an average of 27.41 mm. The largest and smallest specimens are both from the SAM. At Nilpena length measurements of 333 specimens range from 4.61 to 131.25 mm, with an average of 27.45 mm (Table 1). The size frequency distribution (sfd) of all of the Nilpena specimens is right skewed (Fig. 7a). The Sahpiro-Wilk test indicates that the overall size distribution at Nilpena is log-normal.

Bed	Number of Specimens	Area (m2)	Specimens per m2	Distribution	BIC	ΔBIC	Skew
WBSf	328 (280)			log normal	1, EEE	14.7	right
MM3	206 (168)	21.25	9.69	log normal	1, EEE	11.1	right
1TFB	24 (21)	5.62	4.27	niether	n/a		right
MM5	10 (9)	11.29	0.89	log normal	n/a		small
1TLS	11 (9)	2.07	5.33	normal	n/a		small
1TBOF	14	2.33	6.01	niether	n/a		small
STCI	38 (35)	14.53	2.62	niether	n/a		small
Gully Bed	13 (10)	1.08	12.05	normal	n/a		small
STCB	10 (8)	11.3	0.88	normal	n/a		spread
STCJ	14 (13)	11.63	1.2	log normal	n/a		spread
STCX	20 (14)	9.35	2.14	log normal	n/a		spread
STCHI	9 (8)	2.5	5.2	niether	n/a		cluster

Table 1. Distribution, density and size trends for 11 of the 19 beds from the WBSf at Nilpena.

A. Nilpena All
N=328
M=27.5
SD=18.4

B. MM3
N=153(142)
M=24.4
SD=12.9

C. 1TFB
N=21
M=20.87
SD=26.4

D. MM5
N=9(8)
M=23.8
SD=5.5

E. 1TLS
N=12(10)
M=21.6
SD=6.8

F. 1TBOF
N=12
M=11.6
SD=9.8

G. STCI
N=35
M=17.7
SD=3.5

H. Gully Bed
N=11(8)
M=24.5
SD=5.4

I. STCB
N=8(7)
M=59.1
SD=26.8

J. STCJ
N=13(11)
M=41.3
SD=20.8

K. STCX
N=14(9)
M=56.1
SD=24.8

L. STCHI
N=8
M=53.2
SD=6.9

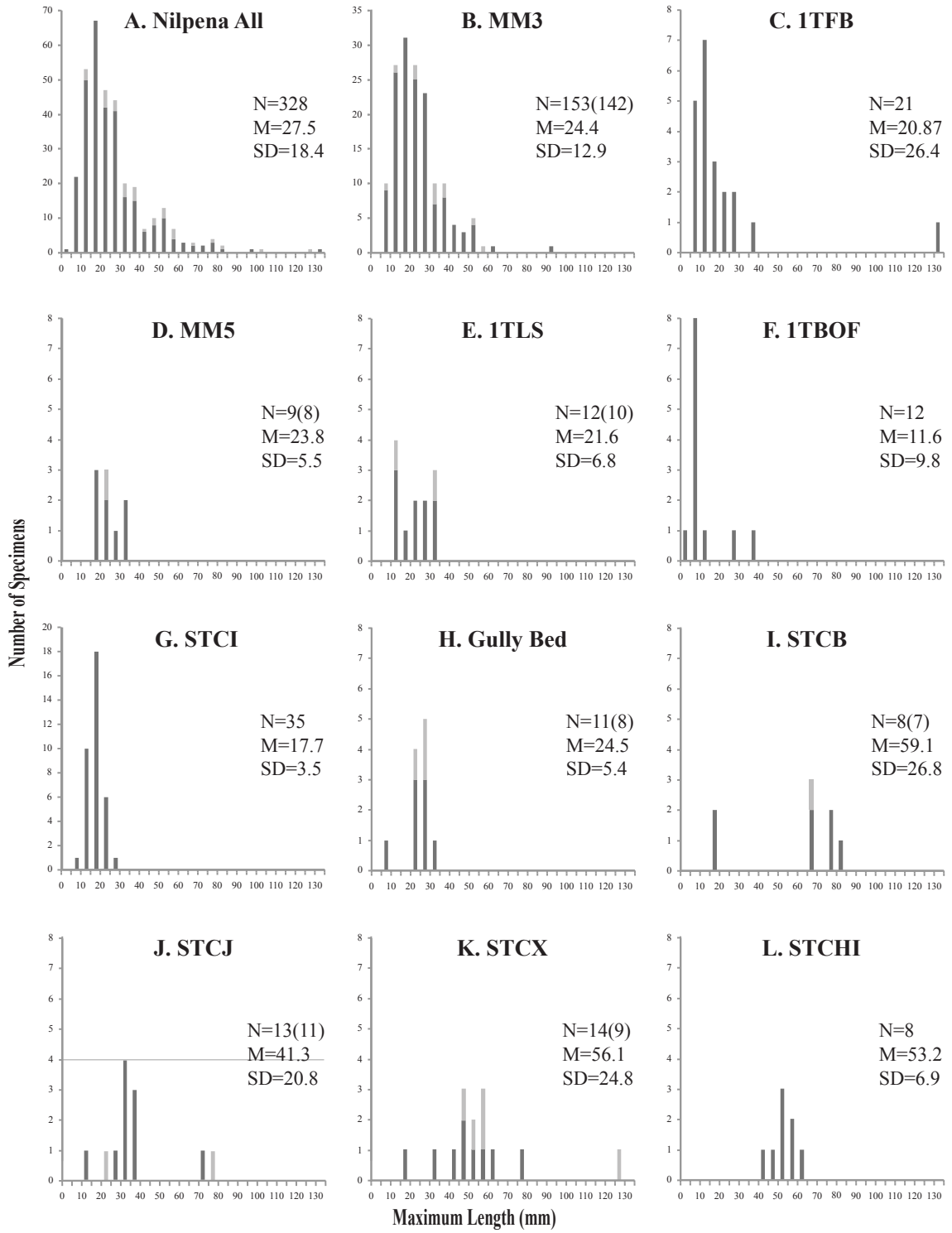Number of Specimens

Maximum Length (mm)

Figure 7. Size frequency distribution of a) all specimens from Nilpena, and b-l) specimens on individual beds. Size is based on maximum length measured along the midline. Dark grey indicates specimens for which length measurements were attainable and light grey indicates calculated lengths based on the length vs. width equation determined by Sperling et al. (in press). Specimen number (N), with total measurable in parentheses, mean (M) and standard deviation (SD) are included for reference.

Facies Distribution

      Dickinsonia occurs in all five fossiliferous facies at Nilpena (Gehling and Droser, 2013). Between the two facies with excavated surface areas, the abundance of *D. costata* is almost an order of magnitude greater in the WBSf than the Sheet-Flow Sands facies (Gehling and Droser, 2013). When normalized for exposed surface area *D. costata* has a greater density in the WBSf. The major difference between these facies is best understood in terms of individual bed abundance and density. *D. costata* in sheet-flow sands consistently show < 0.5 specimens per m^2 and no bed contains more than 3 total specimens. In the WBSf, some beds contain similarly low specimen numbers, but bed densities commonly reach > 5, and up to 12, specimens per m^2. A single bed within this facies contains 206 specimens. Distinct bedding planes are not available in the Shoreface Sand, Delta-Front Sand or Mass-Flow Sand facies, hence, abundance is determined from isolated specimens. In these facies relative abundance compared to other fossils indicates that *Dickinsonia* was relatively uncommon (Gehling and Droser, 2013).
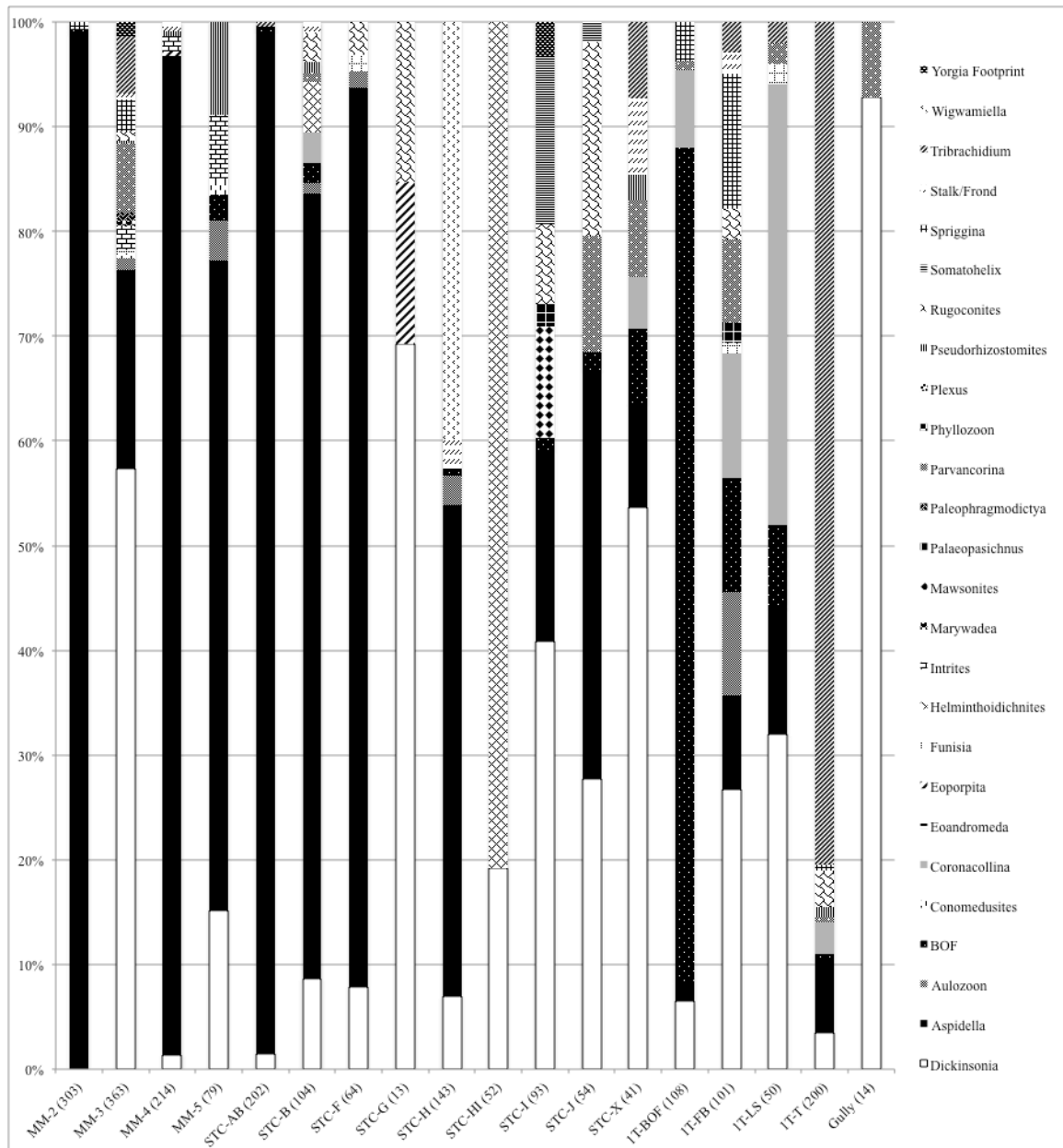
Figure 8. The relative abundance of fossil taxa, including all *Dickinsonia* on 18 excavated beds at Nilpena. Total number of fossils on each bed is given in parentheses after the bed name. All the beds shown represent deposition in the WBSf. The body fossil *Funisia dorothea* is found on beds MM2, STCAB, and STCX in abundances that range in the thousands, and thus, these fossils actually dominate beds. However, their dense packing and poor preservation do not allow accurate counts on these beds (edited from Gehling and Droser, 2014).

Wave-Base Sand facies

Dickinsonia costata occurs on 18 of 19 excavated bedding surfaces in the WBSf. Despite the ubiquity of specimens within this facies, the abundance and density of *D. costata* is highly variable from bed to bed. Excavated beds from the WBSf range in size from over 21 m^2 to approximately one m^2 (Table 1). Bed MM3 contains 206 *D. costata,* while all other beds contain less than 40, and several beds contain less than five specimens. Densities of *D. costata* range from over 12 specimens per m^2 to less than a single specimen per m^2 on several beds. Sizes of specimens within populations are unevenly distributed with average sizes ranging from about 11.5 mm to over 59 mm.

Within the WBSf *D. costata* occurs in association with a number of different taxa. *D. costata* dominates four beds (> 50% of the total population) and occurs with all representative taxa of the White Sea assemblage (Fig. 8).The other taxa found within this facies are heterogeneously distributed (Droser and Gehling, 2015).

Dickinsonia costata occurs with most forms of TOS and other Ediacara biota, but it is absent from bed MM2, which is characterized by the presence of several hundred specimens of the holdfast *Aspidella* and a surface of densely packed felled tubular fossils *Funisia dorothea,* forming a thick and variable TOS. This fossil association is also present on bed STCAB which has only three specimens of deformed *D. costata.* Bed STCX also exhibits abundant felled *F. dorothea,* but does not contain densely packed *Aspidella.* This bed contains twenty *D. costata,* as well as other taxa such as *Parvancorina* and *Tribrachidium.* The few specimens on bed STCAB and the specimens on STCX are all distorted or poorly preserved compared to other bed surfaces (Fig. 9a).

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Other than those with *Funisia,* most beds have variable TOS covering. Beds MM3,

1TFB, STCB and STCJ all contain TOS cover ranging from 30% to nearly 100%. Beds

MM5, 1TLS, STCI and Gully contain < 10% TOS. On Bed STCHI, *D. costata* represents

the only body fossil, but the trace fossil *Helminthoidichnites* is also abundant.

Bed 1TBOF is uniquely dominated by the fossil bundle of filaments, which has

been tentatively interpreted as algae (Xiao et al., 2013). Along with anomalously small *D.*

costata, bed 1TBOF contains only relatively small specimens of *Spriggina* and

Parvancorina.

In addition to several *D. costata*, Bed MM5 contains abundant specimens of mop.

On bed MM5 *D. costata* occurs on top of mop (Fig. 9b). This relationship could only

result from the formation of the mop structures during an event prior to colonization by
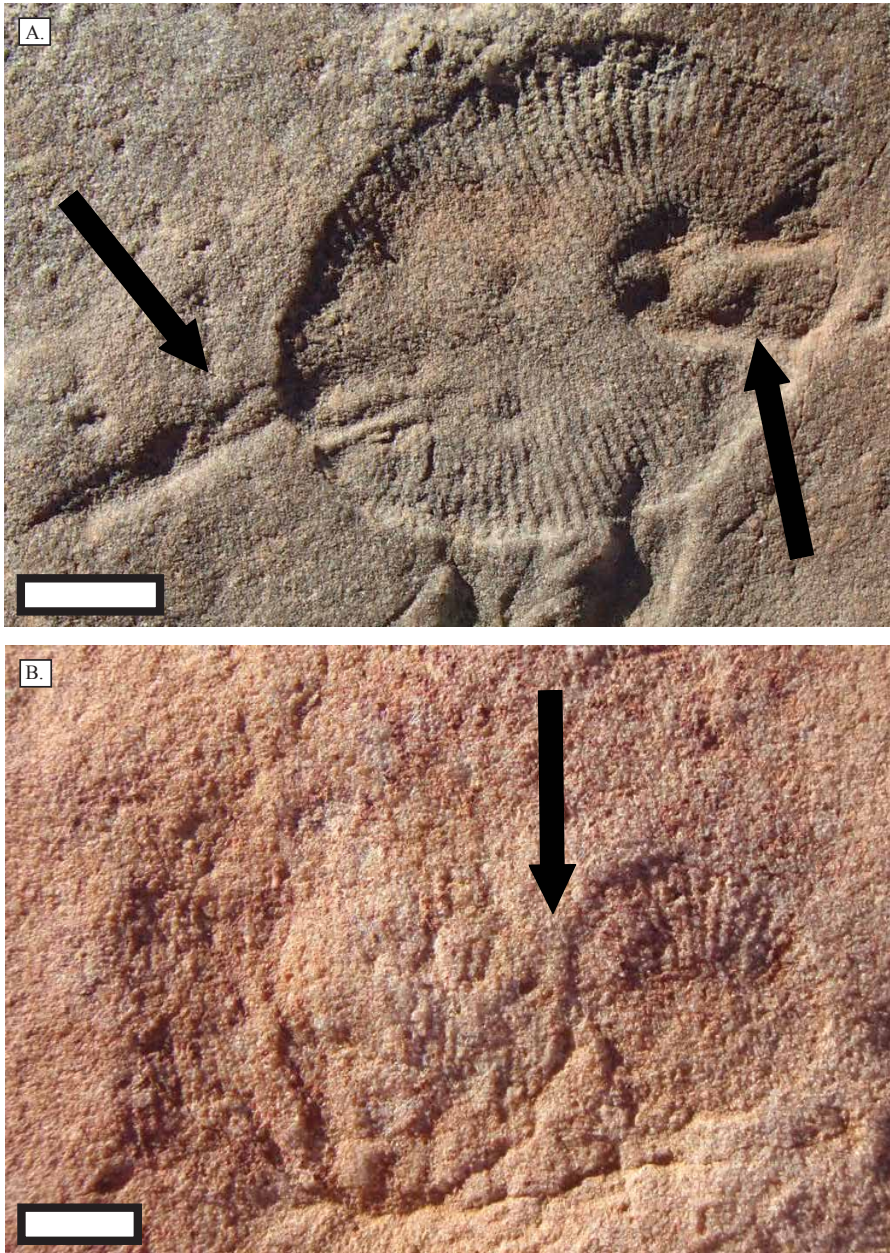
D. costata.

Figure 9. Specimens of *D. costata* on excavated bedding planes from Nilpena. A) Specimen from bed STCX with arrows indicating the 'draping' of specimens over felled tubular fossils. B) Specimen from bed MM5 with arrow indicating the relation of *D. costata* (right) overlapping mop (left).
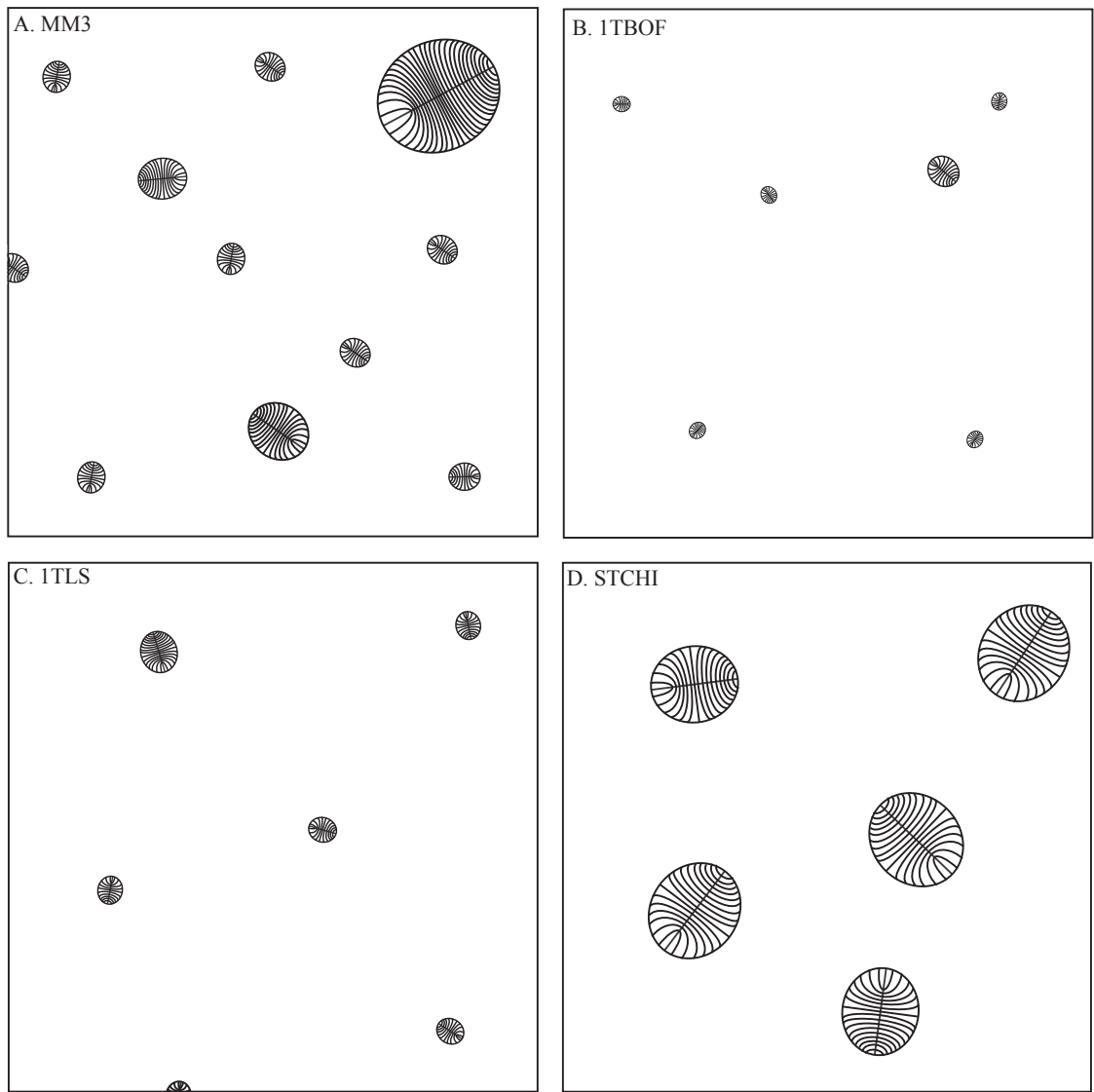
Figure 10. Cartoon populations representative of the sfds found at Nilpena. Each square represents the average number of specimens present within one square meter on each bed, with sizes exaggerated three times actual size based on a meter by meter grid. Sizes of individual specimens are to scale relative to each other.

Size Distributions

Eight of the 18 *D. costata* bearing beds of the WBSf containing more than ten measurable specimens were further analyzed based on their size frequency distributions (sfds). Three beds, MM5, STCB and STCHI, were added to this analysis as they contain distinct sfds and environmental settings that are relevant to this examination. Low specimen numbers on several of these eleven beds result in statistically insignificant results. Data from these beds, as well as for all Nilpena specimens, are summarized in Table 1. Examination of sfds from these eleven beds reveals several trends (Fig. 10). Two beds exhibit right-skewed distributions, MM3, having the greatest number of specimens, and 1TFB (Fig. 7b,c, 10a). Beds MM5, 1TLS, 1TBOF, STCI and Gully all contain populations that are within the smallest and most common sizes known for *D. costata,* with most specimens ranging from 10 to 20 mm, none > 36 mm, and mean values varying from 11.6 to 24.5 mm (Fig. 7d-h, 10b,c). Beds STCB, STCJ and STCX contain virtually the full range of known sizes for *D. costata*, each including at least one specimen < 20 mm and > 75 mm. These beds also contain "clusters" of six to ten specimens at various sizes and mean sizes at least 15 mm > the average for *D. costata* (Fig. 7i-k). Bed STCHI contains no small *D. costata*, with all specimens between 42 and 65 mm (Fig. 7l, 10d).

The Shapiro-Wilk test suggests log-normal distributions for MM3 and STCX. Beds 1TFB and STCI show neither a normal nor log-normal distribution (p-values < 0.05 for both logged and unlogged data). For all specimens within the WBSf, BIC analysis indicates that this distribution represents a single size cluster (difference in BIC for all

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other groupings > 10 for all models). This analysis used only 280 specimens with 136 of those from bed MM3. Multivariate BIC was conducted on all beds and only bed MM3 returned conclusive results. BIC indicates the distribution on bed MM3 represents one size grouping.

Discussion

In modern settings, environmental conditions, such as energy, substrate and disturbance frequency, as well as biological characteristics, including reproductive strategies, control both spatial and size frequency distributions (e.g. Levitian, 1991; Allen et al., 2006). Abundance data show that *Dickinsonia costata* is rare within the Shoreface Sand, Sheet-Flow Sand, and Mass-Flow Sand facies, relatively uncommon in the Delta-Front Sand facies, and relatively abundant in the WBSf (Gehling and Droser, 2013). The densities of *D. costata* in individual populations within the WBSf are unevenly distributed. These data suggest that the shallow marine wave base environment was the preferred habitat for *D. costata,* along with most other members of the White Sea assemblage (Gehling and Droser, 2013). The other four facies represent marginal environments for *D. costata*. The overall size distribution for *D. costata* in the WBSf is clearly right-skewed, indicating that there were many small organisms with decreasing numbers reaching larger sizes. Specimen density displays an order of magnitude difference in populations within the WBSf. Size distributions also vary between beds. Studies of sfds have been previously used to determine biological controls on body size distribution of other Ediacaran forms, such as continuous versus seasonal reproduction (Darroch et al., 2013; Hall, 2015), and asexual versus sexual reproduction (Droser and

Gehling, 2008). Additionally, the large abundance and widespread distribution of *D. costata* within the WBSf allows us to evaluate how different environmental conditions regulated the structure of individual populations.

Environment

Substrate – Associations with other Ediacara taxa and certain mat surfaces demonstrate distinct controls on the abundance and size of *D. costata*. The absence of specimens on bed MM2 and low numbers of specimens on STCAB suggests that this seafloor community, consisting of densely packed frondose and tubular organisms, was not easily inhabited by *D. costata*. The relative deformation of *D. costata* on STCAB further suggests that this was not a preferred environment and the few specimens present existed on top of a highly irregular surface. It appears that movement through closely-associated fronds and tubular organisms was problematic for *D. costata*. This finding suggests that substrates within the WBSf were limiting to *D. costata*.

Bed STCX contains a surface similar to MM2 and STCAB without widespread *Aspidella* and containing relatively large *D. costata.* Despite the relatively high abundance of specimens, this bed was not favorable for smaller individuals due to the ubiquitous presence of tubular fossils on this surface. The draping and distortion of specimens reveals that the dense population of *F. dorothea* that initially populated this surface were toppled, creating a unique organic substrate and allowing *D. costata* to move into the area on top of the felled tubular community. While we do not know how *Dickinsonia* moved, the preferential presence of larger specimens is likely due to difficulty navigating through the dense felled tubes on bed STCX. Thus, the absence of

Aspidella created a more hospitable environment for *D. costata* than on MM2 and STCAB*,* but remained selective toward larger-sized *Dickinsonia*. The presence of *Tribrachidium* and *Parvancorina*, both on the order of 1-2 cm in size, indicates that the absence of small *Dickinsonia* is not taphonomic.

Among beds with "small" populations, bed 1TBOF is an outlier because it is characterized by extensive algae and contains relatively small fossils of many taxa. Lui et al. (2013) interpreted an anomalously small community of rangeomorphs as populations dominated by juvenile forms. This 'nursery' scenario is extremely similar to the small distributions observed for *D. costata*, especially on 1TBOF. Modern ecological studies have noted preferential larvae settlement based on cues related to certain types of biofilm cover (Hadfield, 2011). *D. costata* and possibly other taxa seemed to have preferentially colonized an algal dominated setting. The distribution of larger specimens on bed STCX as well as the small specimens on bed 1TBOF demonstrates that certain sizes of *D. costata* are distributed preferentially based on the environment and substrate. *Environmental disturbance* – The amount of time a bed was exposed prior to burial was a major factor controlling the sizes of *D. costata* preserved. Populations of small sized *D. costata* occur on beds MM5, 1TLS, STCI and Gully. None of these beds have well-developed TOS, indicating that an environmental disturbance – in this case bed smothering – precluded the full development of the community. We attribute the small specimen size found on STCI to an insufficient amount of time for organisms to reach maturity. Bed MM5 contains a similar population of small *D. costata*, an immature community as well as mop. The occurrence of *D. costata* on top of mop suggests that a

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large storm event removed fronds from this surface without deposition and a community of *D. costata* secondarily colonized MM5. Similar to bed STCI, this secondary population had insufficient time to fully develop before burial.

Populations of *D. costata* that contain a broad spectrum of sizes have both right-skewed sfds (beds MM3 and 1TFB) and have 'clusters' of similarly sized specimens greater than the average size of *D. costata* (beds STCB and STCJ). These beds all exhibit evidence of well-developed organic mat surfaces, suggesting that these communities had sufficient time between disturbances for populations of *D. costata* to fully develop.

Reproduction

Reproduction is one of the major controls on size distribution in modern marine environments (ex. Levitan, 1991) and controlled the sfd of *D. costata*. The log-normal, right-skewed distribution of *D. costata* is interpreted as "high infant mortality" a strategy expected for a soft-bodied, mobile invertebrate (Brenchley and Harper, 1998). This reproductive strategy, wherein an organism produces abundant offspring with few expected to reach adulthood, demonstrates a significant biologic control on the sfd of *D. costata*.

Seasonal vs. Continuous Reproduction – Two main reproductive hypotheses are considered for *D. costata:* continuous and seasonal recruitment; both have been determined for other members of the Ediacara biota (Darroch et al., 2013; Zakrevskaya, 2014; Tarhan et al., 2015; Hall, 2015). While we cannot definitively rule out asexual reproduction we have seen no evidence of budding or fragmentation in almost 1,000 specimens, nor has it been previously reported.

We use bed MM3 as a baseline for examining recruitment periodicity, since it has the greatest number of specimens. The continuous reproduction model best explains the sfd on this bed containing a population having a log-normal sfd and a single cluster spanning most of the known size range for *D. costata*. This distribution has a range of sizes that are not clustered. The continuous reproduction hypothesis is supported by the right-skewed distribution on 1TFB. Beds with small populations fit this model as immature, continuously reproducing populations. The remaining four beds, those with distinct clusters and larger mean sizes, are not representative of the expected sfds for continuously reproducing organisms. These anomalous distributions could be due to low specimen numbers, as all of these beds contain less than 20 specimens. There are also possible biological and ecological explanations. Many marine organisms that reproduce continuously will have seasonal periods of more intense reproduction, thus producing cohorts of individuals in times of heightened reproductive output (Giese, 1959; Baeza et al., 2013). Alternatively, active recruitment could have been influenced by other environment factors. The expected abundance of juvenile specimens is below background levels on STCHI, hence not parsimonious with the continuous reproduction hypothesis. This bed also uniquely contains only *D. costata* and *Helminthoidicnites*, further evidence of an anomolous environmental setting.

Mobility may also be an important factor in local size frequency distributions. Populations composed of large specimens may have migrated to an area without active recruitment, explaining both the low densities and lack of small specimens on these surfaces. Alternatively, these four beds may represent generational cohorts, with the

distribution on bed MM3 being smeared as different generations moved in and out of the area. Limpets, a mobile marine gastropod group that reproduce seasonally, may represent an analogous lifestyle to *D. costata.* In a study examining how human interaction leads to biodiversity loss in limpets across the globe, Espinosa et al. (2014) show size frequency charts that are similar to those observed for *D. costata,* including a right-skewed distribution of *Patella ferruginea* from Galeria, Corsica not unlike that found on bed MM3 (Fig. 4a in Espinosa et al., 2014). Since bed MM3 contains almost an order of magnitude more specimens than all other beds and has a sfd indicative of continuous reproduction, this method of recruitment is most likely for *D. costata.*

Comparison to other Ediacara taxa

Sfds for several other taxa from the Ediacaran have been previously examined and provide data comparable with that for *D. costata*. Darroch et al. (2013) demonstrated that three rangeomorph taxa from Mistaken Point (Newfoundland) reproduced continuously based on log-normal sfds, similar to that found on bed MM3. These assemblages are interpreted to represent preservation in a deep-water setting. The authors attribute this reproductive strategy to the lack of triggers for seasonal reproduction in the deep ocean. While *D. costata* lived in shallow waters, this study demonstrates that other Ediacaran organisms reproduced continuously. Zakrevskaya (2014) investigated several organisms from the White Sea region (Russia) which occur in an environmental setting similar to that of the WBSf at Nilpena and have multimodal sfds evident of seasonal reproduction. Specifically, she identified cohorts of *Dickinsonia tenuis*. While this finding was based on two bedding surfaces, each seemed to show different reproductive strategies, similar

to those presented here for *D. costata*. The study attributed certain observed sfds to the mobility of those taxa.

In South Australia bed surfaces represent dynamic environments with a range of possible developmental modes in the same community. *Funisia dorothea* was characterized by aggregate growth in cohorts, (Droser and Gehling, 2008). Size distributions of the form genus *Aspidella* are right-skewed and represent single groupings based on BIC analysis, supporting the occurrence of continuously reproducing organisms in the same deposits as those investigated for *D. costata* (Tarhan et al., 2014). Tarhan et al. (2014) attributed differences in *Aspidella* morphology to varying TOS. While TOS did not control the size distributions within this group, this study demonstrates that differences in organic mat coverings changed the nature of macroscopic populations in the Ediacaran. Hall (2015) identified individual cohorts for three distinct populations of *Tribrachidium*, indicating seasonal or opportunistic reproduction. The cohort of *Tribrachidium* with the smallest mean size exists on bed MM3 suggesting that some populations were juvenile in a mature community with respect to TOS covering and *D. costata* size.

Conclusion

We have identified multiple environmental and biological controls on the abundance and body size of *D. costata*. Environment, based on differences in facies distributions, represents a first order control on abundance, with the WBSf the preferred habitat for *D. costata*. Within this environment *D. costata* was heterogeneously distributed with densities varying from community to community. Surfaces dominated by

fronds and tubular organisms were unlikely to support populations of *D. costata*. Substrates dominated by tubular organisms excluded smaller specimens, while those with widespread bundles of filaments obviously promoted settlement by juveniles. Time of exposure prior to environmental disturbance limited the size range on certain beds and allowed others to reach full maturity. The overall sfd of *D. costata* suggests that this organism can generally be characterized by a pattern of high infant mortality. Determining seasonal versus continuous modes of reproduction prove difficult due to a number of complicating factors, namely small sample size. The most statistically sound sample population exhibits a sfd characteristic of continuous reproduction. These results fit with biological strategies and environmental conditions demonstrated for other Ediacara taxa and show that the excavated surfaces at Nilpena preserve dynamic communities.

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