# Dickinsonia liftoff: Evidence of current derived morphologies

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## ARTICLE INFO

## 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.

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## 1. 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 (Plate 1).

## 2. 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
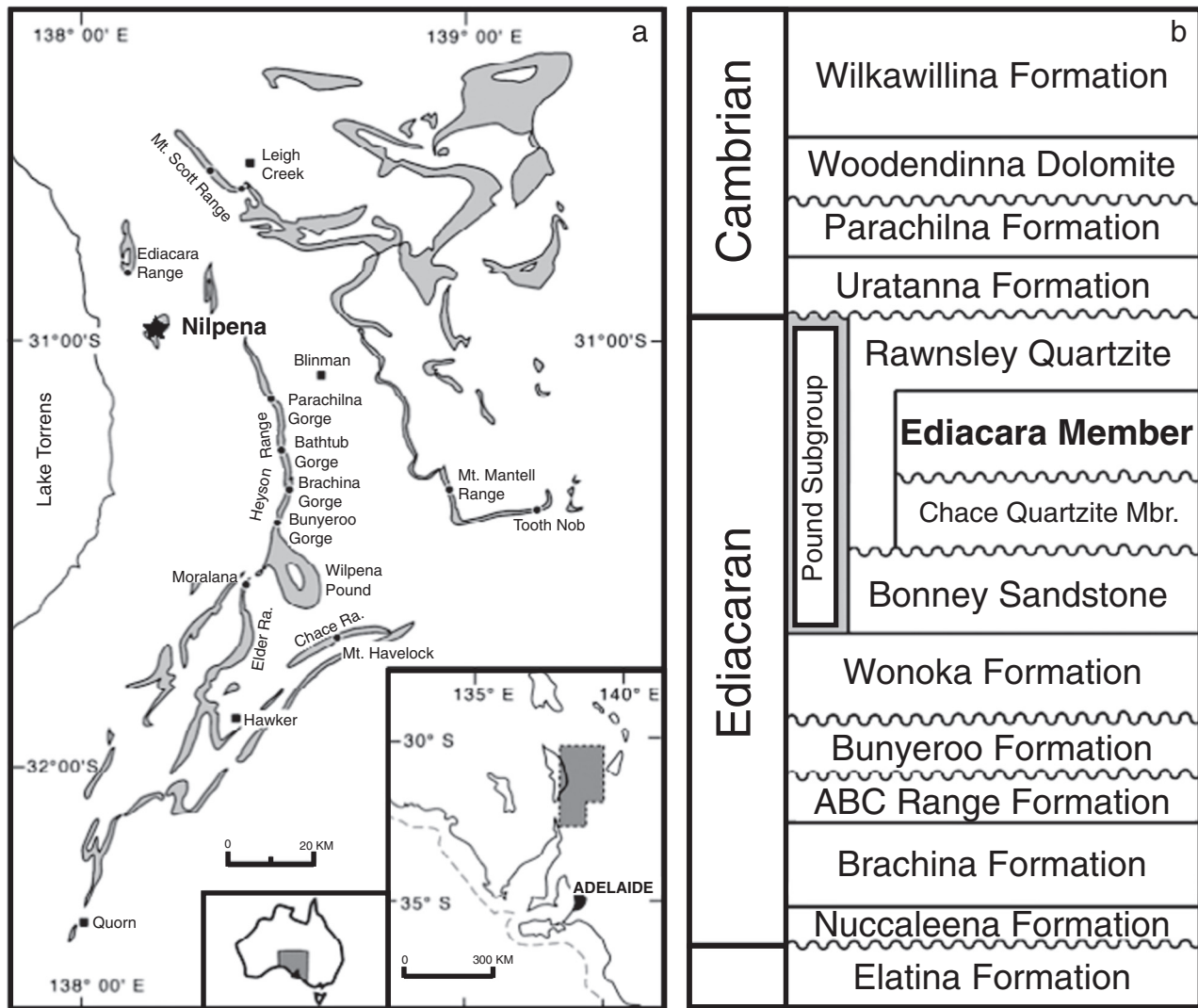
**Fig. 1.** a) Map of the Flinders Ranges showing the Nilpena field locality, marked with the black star; and b) Stratigraphic section showing the position of the Ediacara Member in bold (edited from Gehling and Droser, 2009).

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 m² of in situ material and more than 400 *Dickinsonia*. Three beds, bed MM3, STCI, and STCH, contain *Dickinsonia* exhibiting a unique morphology, with 34% 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).

## 3. *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 (Plate 1a). *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

**Plate 1.** 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.
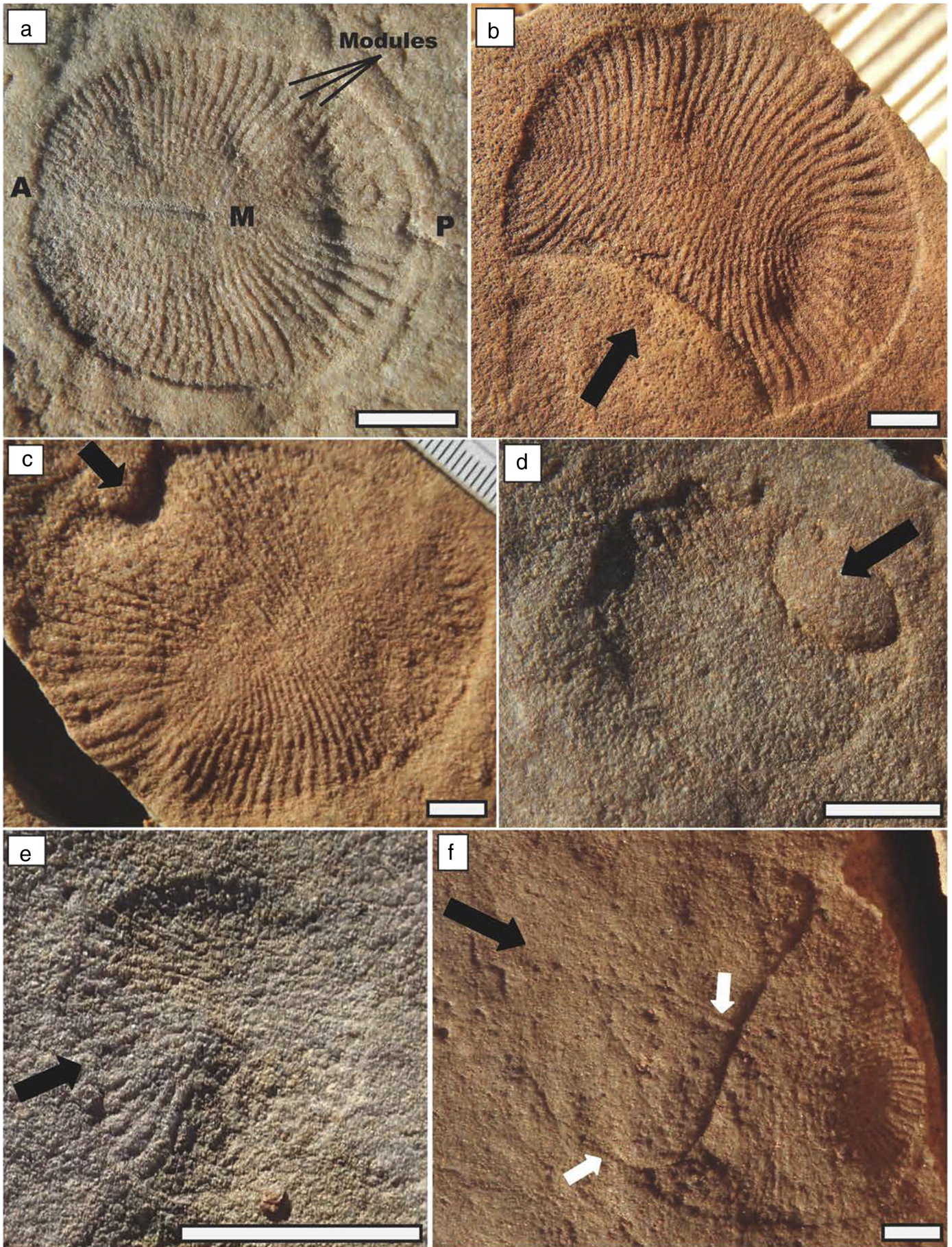
segmentation seen in many modern organisms such as annelids or arthropods, is not known (Sperling and Vinther, 2010).

*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 experiments 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.

## 4. Missing pieces

Over 80 *Dickinsonia* specimens are incompletely preserved (Plate 1b). Specimens can be otherwise well preserved but appear to have a missing piece. This characteristic ranges from extremely small missing portions (Plate 1c, e) to examples were approximately half of the organism appears to be absent (Plate 1f). The missing fragment is expressed in various forms, from round, half circle shaped pieces (Plate 1b, d, e) to v-shaped pieces that appear to have been cleanly cut from the organism (Plate 1c). Despite this morphological variation all specimens identified as incomplete show a smooth re-entrant or straight margin in association with missing portions (Plate 1). In some specimens a faint, ghost like ring appears to outline the incomplete area of the *Dickinsonia* (Plate 1f). 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.

### 4.1. 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. 2a). Of the *Dickinsonia* on bed MM3, 69 are not complete specimens as described above. Orientation measurement of missing portions reveals a nonrandom alignment (Fig. 2b). 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. 2d). 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. 2e).
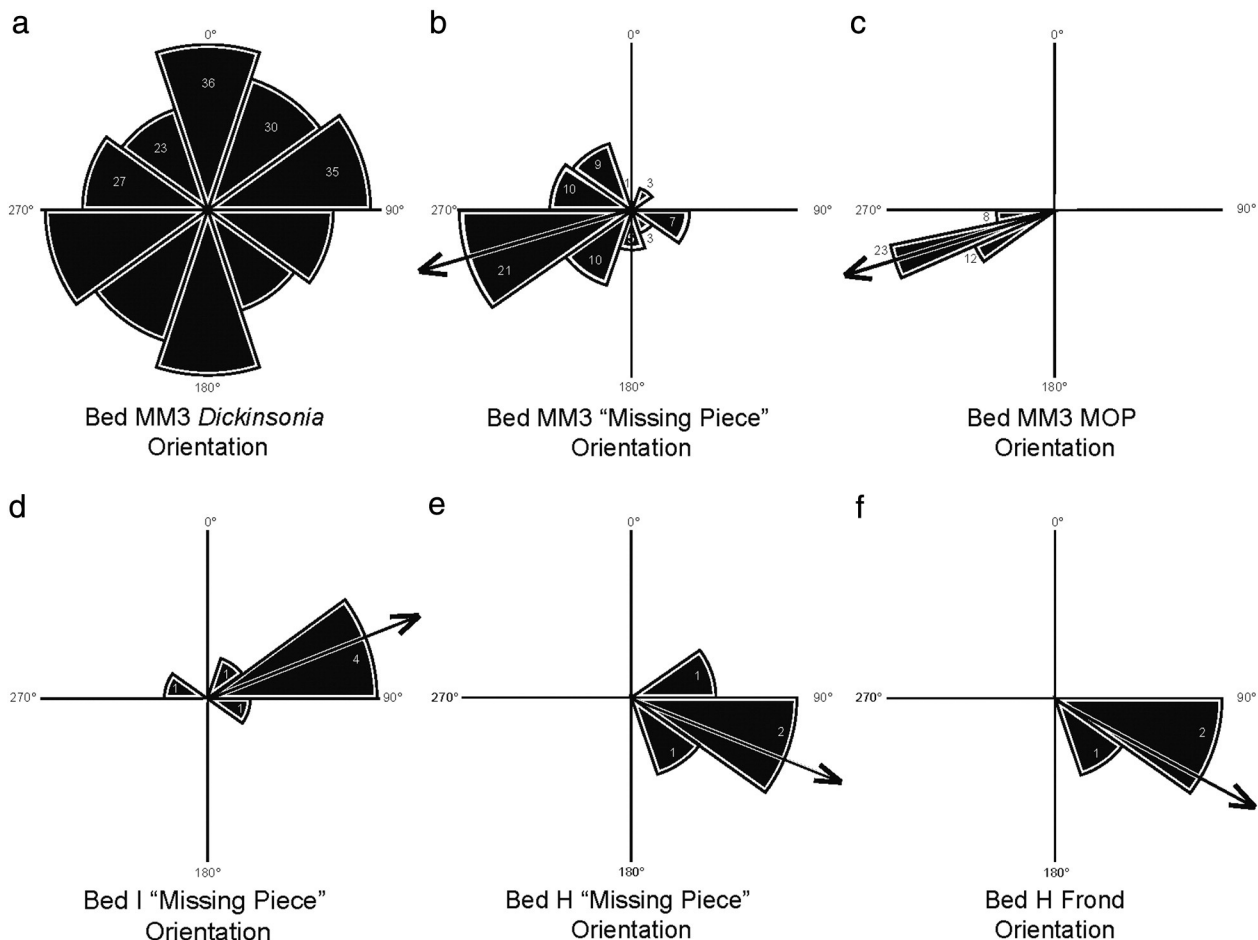


**Fig. 2.** Rose diagrams for orientations of; a) *Dickinsonia* main body axis from bed MM3; b) missing pieces of *Dickinsonia* from bed MM3; c) mop specimens from bed MM3; d) missing pieces of *Dickinsonia* from bed STCI; e) missing pieces of *Dickinsonia* from bed STCH; and f) toppled fronds from bed STCH.

## 4.2. 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. 2c) is consistent with that found for *Dickinsonia* missing pieces from the same bed (Fig. 2b). Bed STCH includes toppled fronds that are preserved with their holdfasts (Fig. 3). Despite low specimen numbers, these felled organisms are also strongly aligned (Fig. 2f). Again, the alignment of the missing pieces of *Dickinsonia* and that found for these fronds are parallel (Fig. 2e, f).

## 5. 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 (Nagle, 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 support 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. 4a). This 'normal' life-position would have been disrupted during storm events as associated currents lifted part of the *Dickinsonia* off of the seafloor (Fig. 4b) allowing the transported sediment to accumulate beneath the lifted portion of the specimen (Fig. 4c). 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.

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 Malakhovskaya, 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
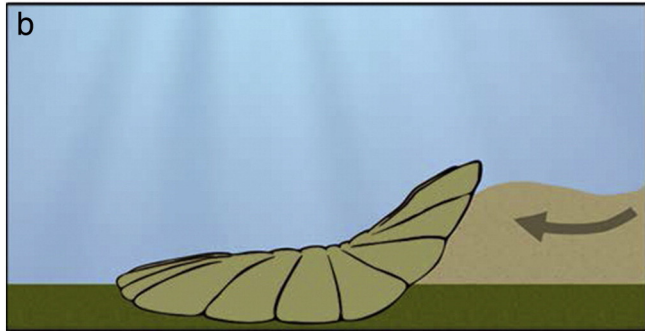


**Fig. 3.** Toppled fronds from Bed H outlined in chalk with arrow indicating current direction.
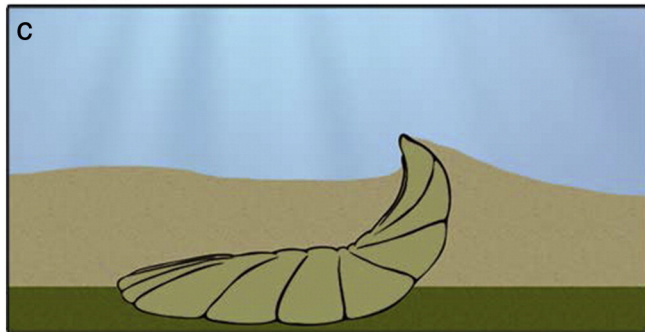
## Life Position
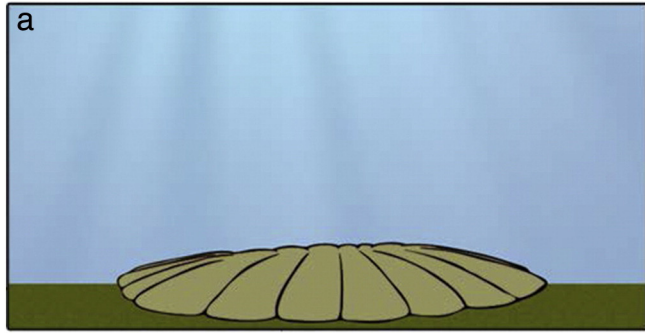
## Storm Event

## Burial

**Fig. 4.** 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.

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.

## 6. 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.

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