

A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes

Erik A. Sperling* and Jakob Vinther

Department of Geology and Geophysics, Yale University, New Haven, CT 06520, USA

*Author for correspondence (email: erik.sperling@yale.edu)

SUMMARY *Dickinsonia* is one of the most recognizable forms in the Ediacaran fauna, but its phylogenetic position has been contentious, and it has been placed in almost every kingdom of life. Here, it is hypothesized that the affinities of *Dickinsonia* lie with the Placozoa (Metazoa), an understudied phylum that is widespread in tropical seas worldwide. Modern placozoans show obvious differences in size and axial organization compared with *Dickinsonia*, but these differences can be accounted for by the stem-group/crown-group distinction. The affinity with placozoans is evidenced primarily by the unique feeding mode of *Dickinsonia*, which is demonstrated by a series of feeding traces. These traces indicate that *Dickinsonia* moved over the Ediacaran matgrounds, and digested the mat using its entire lower sole. The ability of *Dickinsonia* to move negates an algal,

fungal, or sponge affinity, while the feeding mode, external digestion with a ventral sole, rules out placement within any sponge or eumetazoan lineage. The only organisms that both move and feed in this manner are placozoans. Recent molecular phylogenetic studies have demonstrated that placozoans lie above sponges but below Eumetazoa. We hypothesize that *Dickinsonia* and other externally digesting Ediacaran forms are either stem-placozoans, or a series of extinct lineages above sponges and below eumetazoans on the metazoan tree. We discuss the potential evolutionary transitions between the main metazoan feeding modes in the context of the emerging molecular phylogeny, and suggest that aspects of the sponge and placozoan feeding strategies are relicts of nonuniformitarian Proterozoic ocean conditions.

INTRODUCTION

An iconic member of the Ediacaran fauna, *Dickinsonia*'s phylogenetic position has been contentious. It has been allied with many different animal groups including medusoid (Sprigg 1947) and polypoid cnidarians (Valentine 1992), ctenophores (Zhang and Reitner 2006), “of coelenterate grade” (Brasier and Antcliffe 2008), and annelid worms (Wade 1972). In addition it has been referred to other biological kingdoms such as lichen or fungi (Retallack 1994, 2007), the extinct Vendobionta (Seilacher 1989, 1992), and the xenophyophoran protists (Seilacher et al. 2003). Here, the general growth pattern and feeding strategy of *Dickinsonia* is used to place it in a phylogenetic context. Previous interpretations as a triploblastic metazoan are unlikely, due to the lack of any gut, mouth, or anus (Gehling et al. 2005; Brasier and Antcliffe 2008) and the motile mode of feeding through ventral external digestion, which is inferred from series of feeding traces that are associated with *Dickinsonia* body fossils. This recognition that the motile, external digestion feeding mode existed in the Precambrian has important implications for understanding the evolution of metazoan feeding modes.

Dickinsonia terminology

Because the terminology originally used to describe Ediacaran fossils was based on explicit comparisons with modern organisms, workers who do not wish to imply homology with parts or axes of modern animals must strike a balance between using more generally descriptive terms and maintaining continuity with previous literature (Laflamme and Narbonne 2008). In this article we follow Gehling and Narbonne (2007) in using the term module (see Fig. 1A) for an iterated feature of unknown function or origin (“segment” of Wade 1972). We do not imply homology between the modules in *Dickinsonia* and either iterated mesodermal compartments such as those in annelids or the modules present in other Ediacaran fossils. We use the terms front and back (Fig. 1A) in a descriptive sense and do not wish to imply homology with the bilaterian Anterior/Posterior axis; we define the back as the region where modules are added (posterior of Wade 1972). Because the modules at this end are always finer than at the other, the modules are presumably added here and then expand throughout life of the organism. Based on evidence from trace fossils (Gehling et al. 2005), the front is also more or less the direction of movement. When discussing axial properties of both dickinsoniids and placozoans we refer to “sediment-

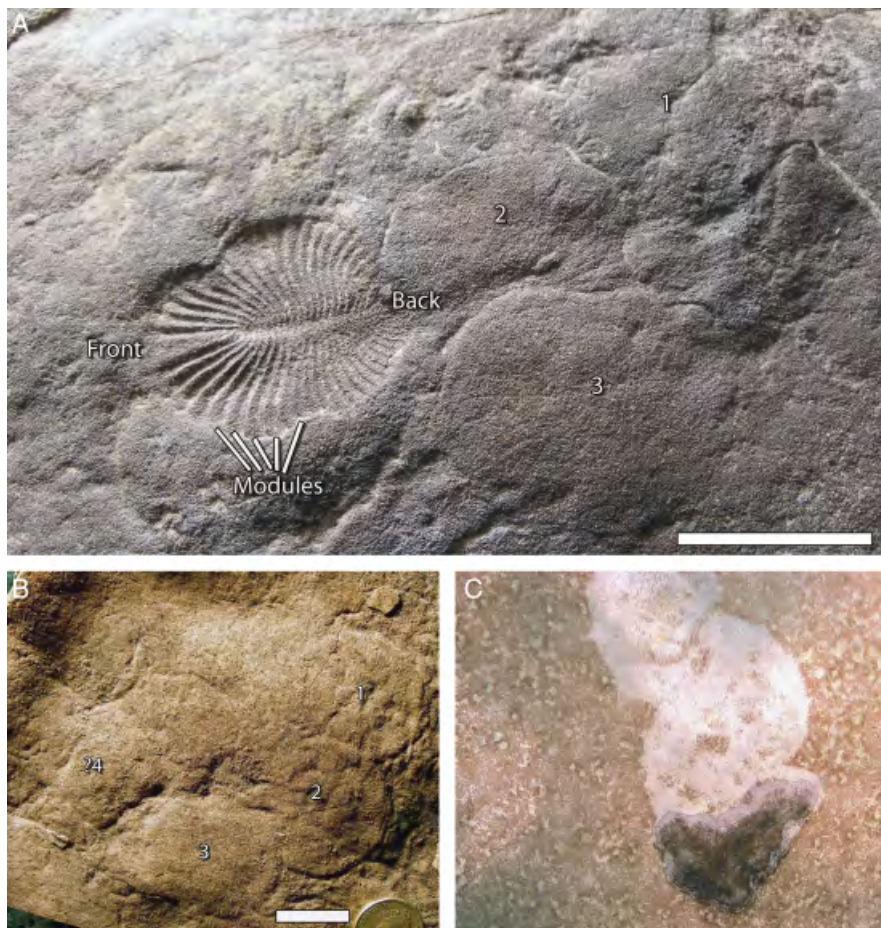


Fig. 1. Body fossils of *Dickinsonia* and feeding traces. (A) Body fossil of *Dickinsonia costata* associated with a series of feeding traces (previously figured by Gehling et al. 2005; South Australia Museum specimen 40845a). Numbers delineate the order of their formation in relation to the body fossil at the end of the series of traces (trace #3 made last). Note the distinct difference in relief between the trace fossils and the body fossil and the overlapping nature between the traces. Terminology used in the article is indicated on the body fossil. Scale bar is 2 cm. (B) Circular series of traces preserving indications of modules and distinct overlap between the traces (previously figured by Gehling et al. 2005; SAM 40844). Along with previously figured specimens (Ivantsov and Malakhovskaya 2002; Gehling et al. 2005; Fedonkin and Vickers-Rich 2007) showing circular movements this demonstrates that the tracks are not current-driven features. Scale bar is 2 cm. (C) *Trichoplax adhaerens* (Placozoa) feeding trace on algal surface in Petri-dish culture. Animal is approximately 2 mm in length.

parallel” and “sediment-perpendicular” planes of symmetry to avoid connotations of homology.

Growth mode

For the best-studied taxon, *Dickinsonia costata*, a growth series can be documented from 12 to 74 modules in small to large specimens. *Dickinsonia* grows by both addition of new modules and continual expansion of pre-existing modules, with the relative importance of module addition versus expansion changing with age. Thus, the body grows in a near isometric fashion in terms of length and width (Runnegar 1982; Retallack 2007), but modules are added at the back at a decreasing rate throughout ontogeny, and body length change is accommodated in part by expansion of previously added modules (J. G. Gehling and E. A. Sperling, personal observation). This contrasts with growth modes in xenophyophoran protists (O. S. Tendal, personal communication) and foraminiferans (Ruppert et al. 2004), which grow to a macroscopic size solely by addition of modules that are larger than subsequent ones, and without expansion of pre-existing modules. Thus, the growth series data demonstrate that

Dickinsonia cannot readily be interpreted as a protist as suggested by Seilacher et al. (2003).

This mode of growth also distinguishes *Dickinsonia* from other Ediacaran fossils whose growth form has been studied, such as *Pteridinium*, which grows by addition of equal-sized modules (Grazhdankin and Seilacher 2002; Laflamme et al. 2009), or *Charniodiscus* and *Fractofusus*, which grow by inflation of modules (Laflamme et al. 2004; Gehling and Narbonne 2007). Because of these differences in growth mode we support Xiao and Laflamme’s (2009) view that the Ediacaran fauna represent a mixture of different clades united by common taphonomic pathways rather than phylogenetic affinity (contra Brasier and Antcliffe 2004), and that the affinities of each Ediacaran taxon need to be considered independently.

Feeding mode

Trace fossils attributed to *Dickinsonia* and *Yorgia* have been found in the Ediacaran of South Australia and the White Sea, Russia, sometimes in association with a body fossil (Ivantsov and Malakhovskaya 2002; Gehling et al. 2005). Body fossils of *Dickinsonia* are preserved as impressions on the base of the capping sandstone beds (i.e., in negative hyporelief), with

preservation likely occurring through the “death mask” mineralization of the ubiquitous seafloor microbial mats (Gehling 1999). The associated traces consist of a series of oval impressions, roughly the same size as the body fossil (if present), and are preserved as originally negative impressions on the seafloor (positive hyporelief). Figure 1 shows some examples from the Ediacaran of South Australia (see also supporting information Fig. S1). The lack of traces in between some of the individual impressions has prompted various workers to argue that they were caused by an organism moving over a firm matground and stopping intermittently to feed using a digestive sole (Ivantsov and Malakhovskaya 2002; Gehling et al. 2005; Seilacher 2007). This digestion of the biomat surface caused a shallow depression, which was filled in during subsequent sedimentation and preserved as a positive feature on the base of capping sandstones. The interpretation of these structures as motile traces greatly reduces the taxonomic possibilities for *Dickinsonia*, as it cannot be a fungus, lichen, alga, or sponge as these organisms are immobile. Further, these traces readily distinguish dickinsoniids from apparently immobile Ediacaran organisms such as the rangeomorphs and ernietta-morphs.

Several lines of evidence point toward these traces being made by a motile organism rather than representing decayed fungal fairy rings (Retallack 2007) or a passive, current-driven feature. The direction of movement can be determined in certain cases through the overlap of successive traces, as younger traces penetrate older traces, and are inconsistent with being a single fungal colony. More importantly, a fungal fairy-ring hypothesis cannot explain why the tracks and body fossil are preserved in opposite relief, or why the “micro-pucker” texture occurs only on the traces and not the body fossil (Gehling and Droser 2009). Nonetheless, these traces could be simply current driven, in essence biological tool marks, and not necessarily indicative of active mobility (McIlroy et al. 2009). However, many of the tracks are not linear, and many are semicircular. Figure 1B, for example, shows three clear traces in a semicircular pattern. This combined with other published photos and illustrations of the traces (Ivantsov and Malakhovskaya 2002; Gehling et al. 2005; Fedonkin and Vickers-Rich 2007) arranged in nonlinear patterns demonstrate that they are unlikely to be current generated.

There are other examples of organisms moving over the Ediacaran matgrounds without leaving a trace until the commencement of active feeding. The ichnofossil *Radulichnus*, for instance, is often found in association with *Kimberella* (Fendonkin et al. 2007), but the traces of the organism moving over the sediment are not preserved, even when the *Radulichnus* traces are found without an associated body fossil and the maker must have moved away (Seilacher et al. 2003). It appears that in the Ediacaran matground world, traces by epibenthic organisms were only preserved when they broke

through the mat to feed or actively removed it, as in *Radulichnus* scrapings or the *Dickinsonia* feeding marks.

SIMILARITIES BETWEEN *DICKINSONIA* AND PLACOZOANS

Dickinsonia appears to feed similarly to a fungus (i.e., saprobically or using external extracellular digestion; Retallack 2007) yet it clearly moves. There is only one group of living organisms that is both motile and feeds using external digestion with the entire ventral surface, the Placozoa (Fig. 1C), which is a lesser-known phylum found in tropical seas worldwide (Voigt et al. 2004; Pearse and Voigt 2007). Placozoans, exemplified by the sole genus *Trichoplax*, are 2–3 mm in diameter and have the general organization of a multinucleate syncytium (fiber cells) sandwiched between an upper and lower cellular epithelium (Grell and Ruthmann 1991; Nielsen 2001). They lack any axis of symmetry, apart from the distinction between an upper protective and a lower feeding epithelium, and they move by ciliary gliding and contraction of fiber cells. Like the inferred feeding mode for dickinsoniids, placozoan feeding is achieved through extracellular digestion, or phagocytosis of algal or microbial biofilms by the ventral epithelium (Fig. 1C; Ruthmann et al. 1986; Wenderoth 1986); we define this feeding mode here as ventral external digestion. Although placozoans are superficially different from dickinsoniids, this feeding mode combined with motility represents a unique feeding mode and body-plan organization, found nowhere else in nature. Combining evidence from both the geological and molecular genetic records, we demonstrate that the differences in size and morphology between crown-group placozoans and putative stem-group placozoans like *Dickinsonia* are not unexpected given paleoenvironmental trends across the Precambrian–Cambrian boundary and the secondary loss of many patterning genes in modern placozoans.

Size differences

Modern placozoans are up to 500 times smaller than the largest dickinsoniid, *Dickinsonia rex*. However, both unique autapomorphies and size changes (unless they violate physiological constraints) are irrelevant for phylogenetic affinities: the position of a taxon is not related to overall similarity, but based on shared derived features (synapomorphies). Differences in size, as well as the lack of modules or a sediment-parallel axis in crown-group Placozoa does not negate a different construction along the stem. *Stegosaurus*, for instance, does not look much like a hummingbird, but yet is certainly a total-group bird (Budd 2001; Donoghue 2005). Ediacaran stem-group placozoans and their allies show a variety of morphologies (e.g., the clearly alternating “modules” of *Yorgia* as compared with the probably linear “modules” of

Dickinsonia), and crown-group placozoans likely represent a limited and highly derived subset of that diversity. The extreme reduction in size and morphology in modern versus Ediacaran “placozoans” may be a by-product of the Cambrian radiation, either from increased predation pressure on the large, defenseless, soft-bodied forms, or through the destruction of their formerly widespread microbial mat food source during the agronomic revolution (Droser and Bottjer 1988; Seilacher and Pflüger 1994; Droser et al. 1999; Bottjer et al. 2000), requiring them to adapt to smaller and patchier biofilms.

Axial differences

Another difference between placozoans and dickinsoniids is that the former is only differentiated along a plane perpendicular to the sediment, whereas the latter have classically been described as bilaterally symmetric (e.g., Wade 1972). However, a number of molecular clues from modern cnidarians and placozoans indicate that bilaterality may have deeper roots than ordinarily considered, and that the lack of overt axes in modern placozoans is unlikely to be primitive. In the sea anemone *Nematostella*, the best-studied cnidarian model system, patterning genes such as those of the Hox family, which are expressed along the anterior–posterior axis in bilaterians, are expressed along the oral–aboral axis. Genes such as Decapentaplegic and TGF- β , which are expressed along the dorsal–ventral axis in bilaterians, are expressed along the directive axis in *Nematostella*, which lies perpendicular to the oral–aboral axis (Finnerty et al. 2004; Matus et al. 2006; Rentzsch et al. 2006; Saina et al. 2009). This molecular evidence, combined with morphological evidence in anthozoans, like the distribution of the siphonoglyph and retractor muscles, suggests that cnidarians are primitively bilateral rather than radial (but see Ball et al. 2007 and Manuel 2009, for more agnostic views of the same molecular and morphological data). If the last common ancestor of eumetazoans was bilaterally symmetric, then bilaterality must have evolved at least along the eumetazoan stem lineage. Furthermore, evidence from gene trees indicates that placozoans have lost many of the ANTP-class (homeobox) genes that are involved in axial patterning in eumetazoans (Monteiro et al. 2006; Peterson and Sperling 2007; Schierwater et al. 2008). This is consistent with a change from a more polarized or differentiated ancestor to a morphologically simpler animal along the placozoan stem lineage. Thus, the greater polarization of *Dickinsonia* (and perhaps true bilaterality) as compared with modern placozoans does not rule out an affinity with this phylum or indeed any position between sponges and triploblasts. This broader conclusion stemming from the genetic complexity of “basal” animals, that apparently bilateral Ediacaran organisms need not be restricted to triploblasts, and

may be deeper on the metazoan tree, was also reached by Erwin (2009).

THE PHYLOGENETIC POSITION OF THE PLACOZOA AND POSSIBLE PLACEMENTS OF *DICKINSONIA*

Ribosomal DNA molecular phylogenetic studies considering placozoans (Bridge et al. 1995; Collins 1998; Medina et al. 2001; Peterson and Eernisse 2001; Wallberg et al. 2004; da Silva et al. 2007) consistently placed placozoans above sponges and below triploblasts on the metazoan tree, but shared little agreement as to their position relative to cnidarians and ctenophores. Recently, three broad-scale phylogenetic studies of metazoans—the genome-scale study of Srivastava et al. (2008), the Expressed Sequence Tag study of Philippe et al. (2009), and a study with seven nuclear housekeeping genes (Sperling et al. 2009)—recovered essentially identical topologies with respect to placozoans, finding the phylum above sponges as the sister group to Eumetazoa (Cnidaria+Ctenophora+Bilateria: Fig. 2). Despite having lost a number of morphological characters such as the extracellular matrix and perhaps the basal membrane, the phylogenetic position of placozoans as sister group to Eumetazoa based on protein-coding genes coincides with that based on cladistic analysis of morphological matrices alone (Nielsen 2001; Peterson and Eernisse 2001). This concordance of independent morphological and molecular datasets strongly supports the phylogenetic position of Placozoa as the sister taxon to Eumetazoa. The inferred feeding mode of *Dickinsonia*, external digestion and nutrient uptake with a ventral sole, combined with its ability to move, is a distinct organization that allies this Ediacaran taxon (as well as other apparently ventrally-digesting forms like *Yorgia*) with the placozoans. Because *Dickinsonia* lacks characters shared by all modern placozoans (such as a single sediment-perpendicular axis), and because it has no apparent characters shared with one clade of modern placozoans to the exclusion of another, it is clearly not a crown-group placozoan. Consequently, the dickinsoniids can most parsimoniously be considered a stem-group placozoan, or as an extinct lineage(s) lying one node higher or lower on the metazoan tree if a ventral digestive epithelium is plesiomorphic for the unnamed clade Placozoa+Eumetazoa (Fig. 2).

THE EVOLUTION OF METAZOAN FEEDING MODES

The motile feeding mode of placozoans, external digestion with a ventral sole, is one of the three general feeding strategies used by animals, along with macrophagy (eumetazoans)

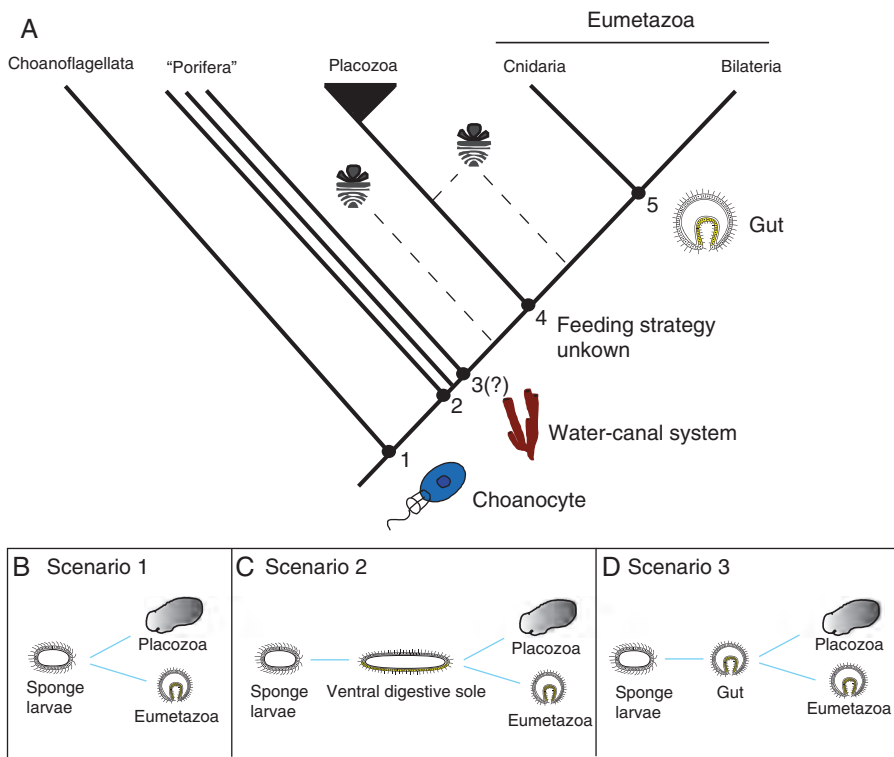


Fig. 2. (A) Diagram of phylogenetic relationships of basal metazoans as summarized from Srivastava et al. (2008), Philippe et al. (2009), and Sperling et al. (2009). Feeding modes are mapped onto the tree where constrained by the phylogenetic topology (nodes 1–3, 5) and marked as unknown where polarity cannot be established (node 4). The paraphyly of sponges (node 3) is an unresolved question and marked with a question mark. Note that the ancestral feeding mode for Metazoa can still be resolved as microphagous even if sponges are monophyletic (Nichols et al. 2009). Possible phylogenetic positions for the Ediacaran taxon *Dickinsonia* and related forms such as *Yorgia* are indicated by dashed lines. These forms likely lie within the animal crown group, above sponges and below eumetazoans, and may be stem placozoans. A position as either stem-eumetazoans or a stem group to the unnamed clade Placozoa+Eumetazoa cannot be ruled out. Crown-group Placozoa is represented on the cladogram as a filled triangle to indicate that dickinsoniids are not crown-group placozoans. Ediacaran forms such as *Dickinsonia* and

Yorgia do not necessarily constitute a monophyletic group and could be separate extinct lineages. (B) Transitional scenario 1 for the evolution of metazoan feeding modes: the last common ancestor at node 4 fed with a water-canal system (or at least microphagously), and no homology exists between the ventral digestive sole of placozoans and the eumetazoan gut. (C) Scenario 2: A ventral digestive sole, similar to those found in modern placozoans, is ancestral for node 4. (D) Scenario 3: A eumetazoan-style gut is ancestral for node 4. This figure appears in color in the online version of this article [DOI: 10.1111/j.1525-142x.2010.00404.x]

and microphagy (sponges). The vast majority of animals (everything from jellyfish to humans) belong to the Eumetazoa, and primitively feed with a gut (macrophagy). The origin of the gut may represent the most important innovation in metazoan history, leading to co-evolutionary arms races that some workers have hypothesized are the ultimate cause of the Cambrian radiation (Stanley 1973; Peterson and Butterfield 2005; Peterson et al. 2005; Butterfield 2007). Sponges, in contrast, feed microphagously using the water-canal system (WCS), a network of chambers containing flagellated cells, choanocytes, whose beating flushes water through the organism. The choanocytes then extract bacteria and dissolved organic carbon (DOC) from the water (microphagy). Other feeding strategies used by animals, such as those in chemosynthetic vent organisms, carnivorous sponges, and absorptive-feeding parasites, are all clearly derived based on their respective phylogenetic positions and do not figure into a discussion of late Proterozoic feeding modes.

Figure 2 summarizes the phylogenetic relationships between “sponges,” placozoans, and eumetazoans, with the feeding modes, where constrained by the phylogenetic topology, mapped onto the tree at appropriate points. Many studies using both ribosomal DNA and nuclear housekeeping genes

have found sponges to be paraphyletic (with varying levels of support), indicating that the adult form of the last common ancestor of animals was benthic, sessile, and fed using the WCS (Cavalier-Smith et al. 1996; Collins 1998; Kruse et al. 1998; Borchiellini et al. 2001; Medina et al. 2001; Peterson and Eernisse 2001; Wallberg et al. 2004; Peterson and Butterfield 2005; Sperling et al. 2007, 2009). In contrast, a recent large-scale study using data from Expressed Sequence Tags found sponges to be monophyletic (Philippe et al. 2009). However, analyses of the phylogenetic signal in nuclear housekeeping genes found that, along with variants of Diploblastica, this may be a phylogenetic artifact, as for a set of seven nuclear housekeeping genes sponge monophyly is only recovered by methods such as Neighbor Joining that generated saturated distances, and by analysis of the fast-evolving sites which are more prone to homoplasy (Sperling et al. 2009).

At node 2, due to the paraphyly of “Porifera,” the last common ancestor of animals fed using the WCS (node 3 marked with a question mark to indicate uncertainty of the phylogenetic topology). Even if sponges were monophyletic, as long as they are the sister group of all other animals, the fact that choanoflagellates also feed with a cilium surrounded by a collar of microvilli still allows for the polarization of

feeding mode and suggests that the last common ancestor of animals at node 2 was a microphagous suspension feeder, if not necessarily using a WCS (Nichols et al. 2009). Although Philippe et al. (2009) suggested that sponge monophyly indicates that the last common ancestor of animals did not have a WCS, this is not strictly true; rather, monophyly simply makes the polarity of the WCS difficult to establish, as the outgroup to Metazoa is unicellular (see fig. 1 of Sperling et al. 2007). At node 5, the last common ancestor of eumetazoans fed macrophagously with a gut. In addition to the monophyly of Eumetazoa, this is supported by gene expression studies that demonstrate that endoderm is homologous between cnidarians and bilaterians (Scholz and Technau 2003; Martindale et al. 2004).

At node 4, corresponding to the last common ancestor of the clade Placozoa+Eumetazoa, the feeding mode is unconstrained by the phylogenetic topology. Three possibilities exist, each equally parsimonious and requiring two separate transitions in feeding mode. Such changes are generally considered to have occurred first in the larval form and then been incorporated into the adult body plan through neotenus evolution (Maldonado 2004; Sperling et al. 2007; Nielsen 2008), although the evidence for this is mainly conjectural. The first possibility is that the ancestor at node 4 still fed with a WCS, or at least microphagously, and there is no homology between the ventral feeding surface of placozoans and the gut of eumetazoans (Fig. 2B). The second possibility is that the ancestor at node 4 fed with external digestion through a ventral sole like modern placozoans, and that the gut was an innovation along the eumetazoan stem lineage (Fig. 2C). The third possibility is that the node 4 ancestor fed macrophagously using a gut, which was lost on the stem-lineage leading to crown-group Placozoa (Nielsen 2008; Fig. 2D). It is notable that although the gut and the digestive ventral sole seem quite distinct, functionally both represent enzymatic digestion in an enclosed space, with digestion taking place within the confines of the endoderm in eumetazoans, and between the ventral sole and the mat surface in the case of modern placozoans (and a hypothetical ancestor feeding with ventral external digestion). The three scenarios can be tested through phylogenetics, as demonstrating that either Placozoa or Eumetazoa is paraphyletic with respect to the other would establish polarity, or through homology assessments stemming from analyses of the gene-regulatory networks underlying development of the choanoderm, placozoan ventral digestive sole, and endoderm.

Rooting metazoan feeding modes in the Proterozoic environment

Microphagy, macrophagy, and motile feeding with a ventral digestive sole all appeared early in metazoan history and must inevitably be rooted in the unique physical and biological

environment of the late Precambrian (Neoproterozoic) world. Evidence from molecular clocks and the biomarker record suggest that this early evolution of feeding modes took place in the Cryogenian (Love et al. 2009; Sperling et al. 2010), in an ocean whose structure and composition was vastly different not only from the modern ocean but from the earlier Neoproterozoic and Ediacaran oceans as well (Canfield et al. 2008; Johnston et al. 2009; Lyons et al. 2009). The origin of morphological structures must be placed in their paleoenvironmental context (e.g., Peterson 2005), and although modern placozoans show clear evidence of morphological loss (Jenner 2004), it is not necessarily certain that their feeding mode is highly derived as well.

It is possible that the placozoan digestive sole is one of several feeding modes present in modern animals that are a relict of Proterozoic ocean chemistry and ecology. For example, the ability of modern sponges to obtain a significant percentage of their nutritional requirement from DOC (Rieswig 1974; Yahel et al. 2003; de Goeij et al. 2008a, b) is likely a holdover from a Proterozoic ocean that may have contained orders of magnitude more DOC (Rothman et al. 2003; Sperling et al. 2007). Similarly, the motile feeding mode with a digestive ventral sole (as evidenced by dickinsoniids) arose in a Precambrian ocean where ubiquitous microbial mats covered the seafloor (Hagadorn and Bottjer 1997, 1999; Gehling 1999; Gehling and Droser 2009). Notably, the pervasiveness of the mats does raise the possibility of convergence to feed upon this food source. Convergence to utilize nutrient sources specific to the Neoproterozoic can be seen, for example, in the likely independent evolution of structures designed to exploit the oceanic DOC pool by sponges, rangeomorphs, and erniettamorphs (Sperling et al. 2007; Laflamme et al. 2009). Nonetheless, in the absence of evidence for other affinities, it is most parsimonious to consider the distinct motile life strategy with an external digestive sole to place the dickinsoniids between sponges and cnidarians (possibly as stem placozoans) on the metazoan tree (Fig. 2A). If this hypothesis is correct, the feeding mode of placozoans is another example of a metazoan feeding strategy still present in extant organisms that has its roots in the nonuniformitarian ocean conditions of the Proterozoic.

Intriguingly, it is the gut, which from our anthropomorphic viewpoint is superficially most easy to explain, that is hardest to causally root in the late-Precambrian world. Fundamental questions remain regarding the evolution of the gut: when it originated and whether it arose in the context of an ancestor that fed with a WCS or digestive sole. More data on the timing of divergences between “sponges,” placozoans, and eumetazoans, from both molecular clocks and the geologic record, the homology of metazoan feeding structures, and the paleoenvironments/paleoecology of this time period will be needed to further our understanding of these questions.

CONCLUSIONS

The Ediacaran taxon *Dickinsonia* has endured a controversial taxonomic history, but it can be most readily interpreted as a stem-group placozoan, or as an extinct lineage above sponges and below eumetazoans. Original interpretations as a triploblastic worm, or indeed as a eumetazoan in general, are refuted by the external digestive feeding mode and lack of eumetazoan feeding structures. This cannot be stressed enough—if *Dickinsonia* lacks a gut and mouth and feeds using a ventral digestive sole, as indicated by the trace fossil evidence, it is unlikely to be a eumetazoan. The suggestion by Brasier and Antcliffe (2008) that *Dickinsonia* does not have a gut or mouth, yet is still “of coelenterate grade,” for instance, is illogical.

The existence of an Ediacaran organism (*Dickinsonia*) feeding similar to a placozoan demonstrates the origin of all three feeding modes in the Ediacaran, as there is evidence from fossils (Gehling and Rigby 1996; Martin et al. 2000; Love et al. 2009) and molecular clocks (Peterson et al. 2008; Sperling et al. 2010) that the sponge and eumetazoan feeding modes were also present. Molecular phylogenetic results indicate that the last common ancestor of animals fed microphagously, likely with a WCS, but cannot determine the polarity of change with respect to the placozoan and eumetazoan feeding modes as each is reciprocally monophyletic. Nonetheless, these three feeding modes had their provenance in the unique biological and geochemical milieu of the Neoproterozoic, with the motile ventral-digestive feeding mode of placozoans likely originating on a nonuniformitarian seafloor covered by pervasive microbial mats, and highlights the importance of considering ecological strategies and morphological structures in their original geologic context.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Additional examples of dickinsoniid body fossils (BF) and feeding traces (T). A. Body fossil of *Dickinsonia rex* above. The body is contracted at the right, revealing an underlying feeding trace. Below are two large feeding traces of a different *D. rex*, the fidelity of preservation suggests that the left trace was made first (T1), followed by the right trace (T2), which indicates that the “front end” (see terminology section in main text) is the direction of movement. B. Bodyfossil of *D. costata* that appears highly contracted, revealing an underlying feeding trace (also figured by Gehling et al. 2005). C. Small dickinsoniid body fossil overlapping a feeding trace (also figured by Gehling et al. 2005). D. Dickinsoniid body fossil, left, and a feeding trace of similar sized dickinsoniid, right. E. Two small overlapping feeding traces on a conspicuous “elephant skin” textured biomat surface. Scalebars: A, 5 cm. B, 2 cm. C, 2 cm. D, 10 cm. E, 2 cm.

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