ORGANISMAL BIOLOGY

10.1126/sciadv.1500800

Suspension feeding in the enigmatic Ediacaran organism *Tribrachidium* demonstrates complexity of Neoproterozoic ecosystems

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The first diverse and morphologically complex macroscopic communities appear in the late Ediacaran period, 575 to 541 million years ago (Ma). The enigmatic organisms that make up these communities are thought to have formed simple ecosystems characterized by a narrow range of feeding modes, with most restricted to the passive absorption of organic particles (osmotrophy). We test between competing feeding models for the iconic Ediacaran organism *Tribrachidium heraldicum* using computational fluid dynamics. We show that the external morphology of *Tribrachidium* passively directs water flow toward the apex of the organism and generates low-velocity eddies above apical "pits." These patterns of fluid flow are inconsistent with osmotrophy and instead support the interpretation of *Tribrachidium* as a passive suspension feeder. This finding provides the oldest empirical evidence for suspension feeding at 555 to 550 Ma, ~10 million years before the Cambrian explosion, and demonstrates that Ediacaran organisms formed more complex ecosystems in the latest Precambrian, involving a larger number of ecological guilds, than currently appreciated.

INTRODUCTION

The first morphologically complex eukaryotes appear in the late Ediacaran period [575 to 541 million years ago (Ma)] and represent the first major radiation of multicellular life. These organisms are often collectively referred to as the "Ediacara biota," although they most likely represent a diverse assemblage of eukaryotic groups, including both stem- and crown-group animals, as well as extinct higher-order clades with no modern representatives (*1*–*3*). The record of these organisms predates the Cambrian explosion by ~40 million years and provides critical information concerning evolutionary innovations in early multicellular life forms (*4*). Ediacaran ecosystems are thought to have been relatively simple, comprising few of unique modes of nutrient acquisition and characterized by limited biotic interactions between organisms (*5*). However, ecological understanding of the complexity of Ediacaran ecosystems is likely constrained by limited paleobiological knowledge; the manner in which Ediacaran organisms reproduced, dispersed, or fed is [with rare exceptions (*6*–*8*)] poorly understood. Inferring the feeding strategies of these enigmatic organisms has been particularly problematic because many Ediacaran organisms are characterized by body plans that are radically different from those of extant groups and hence lack any clear modern analogs (*9*). Nevertheless, establishing the feeding modes of Ediacaran organisms is critical to determining their phylogenetic affinities (*10*), the complexity of Ediacaran ecosystems (*11*), and the nature of bioavailable carbon in the water column (*12*). All of these topics are still debated and represent fundamental questions in Precambrian geobiology.

Tribrachidium heraldicum is an iconic soft-bodied Ediacaran organism restricted to shallow-water environments and characterized by triradial (threefold) symmetry, which is entirely unknown among living animal phyla. Consequently, it has resisted paleobiological interpretation, and almost nothing is known about its biology, ecology or the larger role it played in Ediacaran ecosystems. *Tribrachidium* has an approximately hemispherical aspect (typically reaching 2 to 4 cm in diameter) and is constructed from three raised branches that meet at the top of the organism (Fig. 1). The triradial branches curve toward the margin in a counterclockwise direction, becoming parallel to the periphery at the margin of the body (*13*). The primary branches are subdivided into a series of smaller secondary branches, which are roughly perpendicular to the central axes of the primary branches, forming a "tentacular fringe" that extends to the edge of the organism (*14*, *15*). Toward the apex, each primary branch displays a prominent convex "bulla" at the point at which it starts to curve (*14*, *15*). The gaps between bullae and adjacent branches create three shallow circular depressions at the apex of the organism (hereinafter referred to as "apical pits"), which are separated by a Y-shaped protrusion where the primary branches meet. Fossils from South Australia typically have low relief (~2 mm) but show little evidence for deformation (*15*). As a result, *Tribrachidium* fossils are in all likelihood close morphological representations of the living organisms.

Tribrachidium is known only from Ediacaran-aged rocks ("White Sea" assemblage; 555 to 550 Ma) in South Australia, Russia, and Ukraine, where it is locally abundant in shallow-marine siliciclastic sediments deposited within or just below storm wave base (*16*–*20*). It has been best studied from the (largely) shallow-marine successions preserved at Nilpena, South Australia, where it is common in both wave-base and sheet-flow quartz sandstone facies and is most frequently found in moderate abundance [<20 individuals per bed (*15*, *17*)]. The wave-base facies is principally composed of thin-bedded, wave- and current-rippled sandstones, whereas the sheet-flow facies is composed of laterally continuous event beds having planar lamination and tool marks, without ripples (*17*, *20*); this distribution establishes *Tribrachidium* as a relative ecological generalist (*15*), occupying depositional environments that would have been characterized by a range of current velocities. Hypotheses for the evolutionary affinities of *Tribrachidium* have varied widely,

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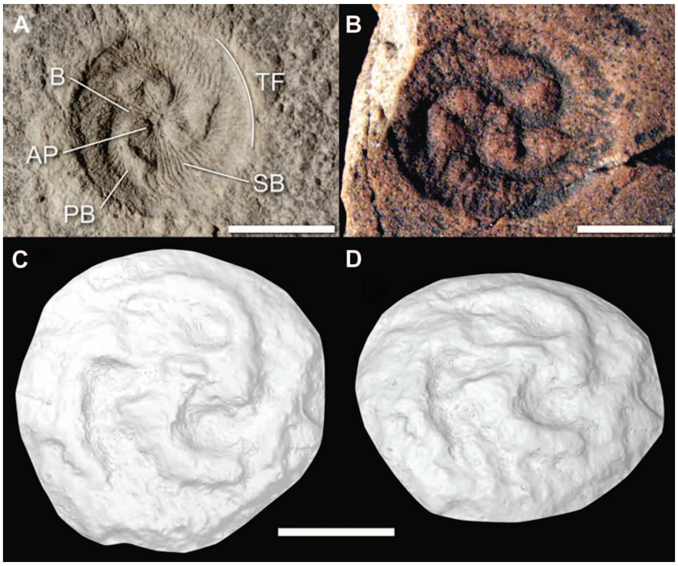

Fig. 1. Morphology and digital reconstruction of *T. heraldicum*. (**A**) *Tribrachidium* specimen N3993/5056 from the Ediacaran (~555 Ma) White Sea area of Russia. (**B**) *Tribrachidium* specimen SAM P12889 (paratype) from the Ediacaran of South Australia (Flinders Ranges). (**C** and **D**) Digital reconstruction of a latex cast of *Tribrachidium* specimen (020N-033W-TBE) from the Ediacaran of South Australia (Flinders Ranges), in upper (C) and angled (D) views. AP, apical pit; B, bulla; PB, primary branch; SB, secondary branch; TF, tentacular fringe. Scale bars, 10 mm.

from either a stem- or crown-group poriferan (*18*, *19*) to a stem-group echinoderm (*13*). However, more recent analyses suggest that the similarities between *Tribrachidium* and these groups are superficial, and *Tribrachidium* is best understood as a multicellular eukaryote with uncertain relationships to crown Metazoa.

On the basis of the known diversity of Ediacaran feeding modes (*5*) and by drawing parallels with extant, shallow-marine sessile macroscopic organisms, two possible feeding strategies can be proposed for *Tribrachidium*: (i) osmotrophy and (ii) suspension feeding. Modern shallow-marine settings can encompass a wide variety of feeding modes, such as photoautotrophy, filter feeding, grazing, burrowing, predation, and deposit feeding. However, Ediacaran shallow-marine settings differed considerably from their Phanerozoic and modern counterparts, due in part to the presence of near-ubiquitous seafloor microbial mats. In these settings, vertical burrowing was apparently absent (and even horizontal burrowing rare by comparison with the Paleozoic), and surficial grazing was restricted to only a few taxa, such as *Kimberella* (*21*–*23*). Seafloor microbial mats allowed unmineralized and frondose epibenthic organisms to anchor themselves to the sediment by means of discoidal holdfasts (*24*). Many of these organisms are thought to have fed osmotrophically [principally Rangeomorpha and Erniettomorpha (*25*)] on the basis that these groups exhibit surface area–to–volume (SA/V) ratios similar to those of modern organisms that feed via passive absorption of dissolved organic matter (principally megabacteria). Filter feeding has been suggested for some of these frondose taxa (*26*) but has not yet been unequivocally demonstrated (*27*). Photoautotrophy is another possibility, although we consider this unlikely because *Tribrachidium* lacks a frond or petalodium that would have served to increase surface area and efficiently harvest sunlight. Although this does not definitively rule out photoautotrophy, few authors have presented any credible evidence to support the inference of either Ediacaran photoautotrophs [other than algae, which are most often preserved as carbonaceous compressions (*28*)] or the presence of photoautotrophic endosymbionts associated with Ediacaran organisms. There is no paleontological or sedimentological evidence that *Tribrachidium* was mobile or actively engaged in mining the sediment for nutrients, and therefore, we reject active predation, grazing, and deposit feeding as possible feeding modes. Thus, osmotrophy and filter feeding appear to be the two most plausible feeding modes for *Tribrachidium*.

Specific predictions can be made for these two hypothesized feeding modes. Macroscopic osmotrophs rely on passive absorption of organic matter through membranes and thus maximize feeding by distributing flow evenly across all exposed exterior surfaces (*25*, *29*). We predict that if *Tribrachidium* fed primarily as an osmotroph, its external morphology would have distributed flow over the entire surface of the organism to maximize the surface area available for nutrient uptake. In contrast, suspension feeders obtain nutrients by transporting water through, or past, structures specialized to entrap organic particles (*30*, *31*). Inference of a suspension-feeding habit would therefore require that the external morphology of *Tribrachidium* concentrated flow toward one or more specific areas of the organism. Flume experiments using the Ediacaran frondose taxon *Charniodiscus* illustrate this distinction (*32*). Singer *et al.* (*32*) demonstrated that in moving fluids, Ediacaran fronds became near-parallel to the direction of current, allowing water to flow along the length of the exposed frond surface; from here, low-velocity flow was directed along primary and secondary canals running across the entirety of the frond, maximizing opportunities for passive uptake of dissolved organic matter (thus supporting osmotrophy). In contrast, if flow around the organism (either low velocity or turbulent flow, which could facilitate particle capture) was concentrated into localized areas, this would instead support a suspension-feeding habit; examples include around the lophophore of a brachiopod or in the turbulent eddies developed above and downstream of sea anemones (*33*, *34*).

To test these predictions, and thus evaluate support for osmotrophy and suspension feeding, we used computational fluid dynamics (CFD) to analyze the hydrodynamic behavior of *Tribrachidium*. This method generates quantitative data based on numerical simulations of fluid flow and is thus independent of assumptions regarding the choice of interpretative model. In this manner, the functional performance of an Ediacaran organism under moving fluids is objectively analyzed.

RESULTS

CFD simulations

A three-dimensional digital reconstruction of *Tribrachidium*, based on an x-ray microtomography scan of a latex cast of a well-preserved fossil collected from South Australia, was used in the CFD analyses (see model S1). The simulations were conducted with *Tribrachidium* at three different orientations to the current (0°, 120°, and 240°), using a range of flow velocities (0.05 to 0.5 m/s) that are typical for shallow-marine settings on the continental shelf (*35*), and which also reflect the diversity of environments that *Tribrachidium* inhabited (*15*). Although exact sediment-bottom current velocities are difficult to infer from preserved sedimentary structures, this range of simulated velocities falls inside the range measured for rippled substrates in modern environments (*36–38*), and thus likely provides a good match for the current velocities typically experienced by *Tribrachidium* in wave-base facies. The results demonstrate that flow velocity decreases rapidly where it first encounters the *Tribrachidium* reconstruction, with a steep velocity gradient (the boundary layer) developing as the flow approaches the lower margin of the simulation volume (Fig. 2, A to L, and figs. S2 to S4). An elongated, low-velocity flow region (the wake) forms downstream of the organism. The size and shape of the wake vary as a consequence of the orientation of the organism to the current and the ambient velocity. Within the wake, a zone of recirculation develops behind *Tribrachidium*; here, low-velocity flow is directed back toward the organism and is channeled by the three raised primary branches up to the apex where small vortices develop within the three circular depressions. This recirculating flow pattern is observable in all the simulations, irrespective of the orientation of *Tribrachidium* to the current, but is noticeably stronger with an ambient velocity of 0.2 m/s or greater (Fig. 2, A to L, and figs. S2 to S4).

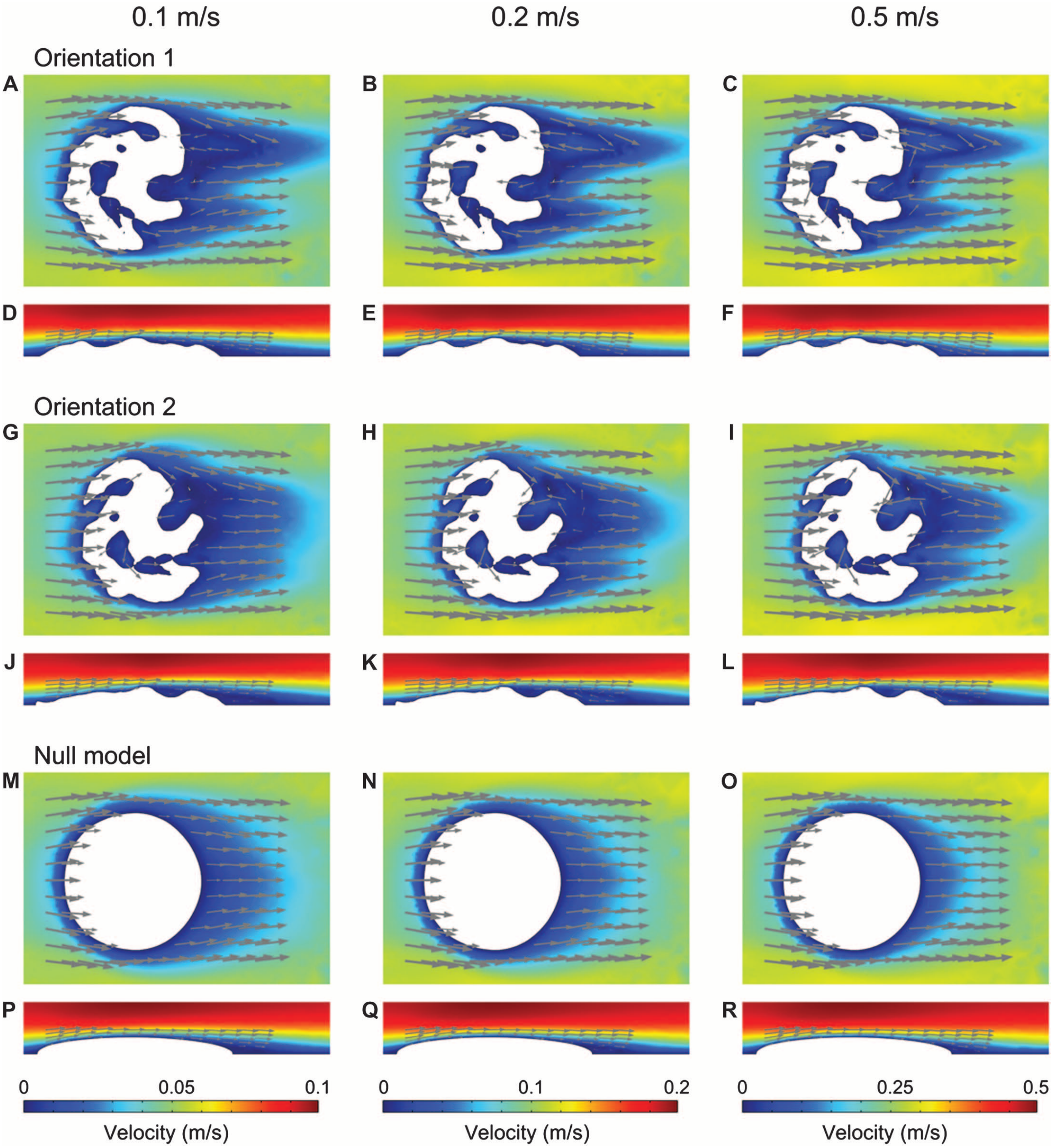

Fig. 2. CFD simulations. (**A** to **R**) Details of water flow around *Tribrachidium* oriented at 0° (A to F) and 240° (G to L) to the current, and a smooth, unornamented hemisphere (null model) (M to R). Results visualized as two-dimensional plots of flow velocity magnitude with flow vectors (gray arrows; length of arrows proportional to the natural logarithm of the flow velocity magnitude), in upper (A to C, G to I, and M to O) and lateral (D to F, J to L, and P to R) views. The ambient flow is from left to right.

To explore the influence of surface geometry on the flow patterns, we repeated the simulations using a smooth, unornamented hemisphere (null model). In these simulations, there is virtually no recirculating flow in the wake downstream of the null model or in any other regions adjacent to it (Fig. 2, M to R, and fig. S5).

Last, although fossil specimens from South Australia show only minor evidence for vertical compaction (*15*), and the height of our scanned specimen (~3 mm) exceeds any of those described by Hall *et al.* (*15*) (suggesting that this individual was not strongly compressed), we cannot rule out the possibility that some postmortem vertical compaction has occurred (and also that the extent of compaction may have varied between fossil localities). Therefore, we performed an additional series of simulations designed to test the effect of original relief above the sediment surface. For three simulated current velocities (0.05, 0.25, and 0.5 m/s), we examined flow patterns around a model *Tribrachidium* with the original height doubled (~6 mm) and a model with the original height halved (~1.5 mm). The results of these additional simulations (Fig. 3) show that the relief of the model plays a strong role in

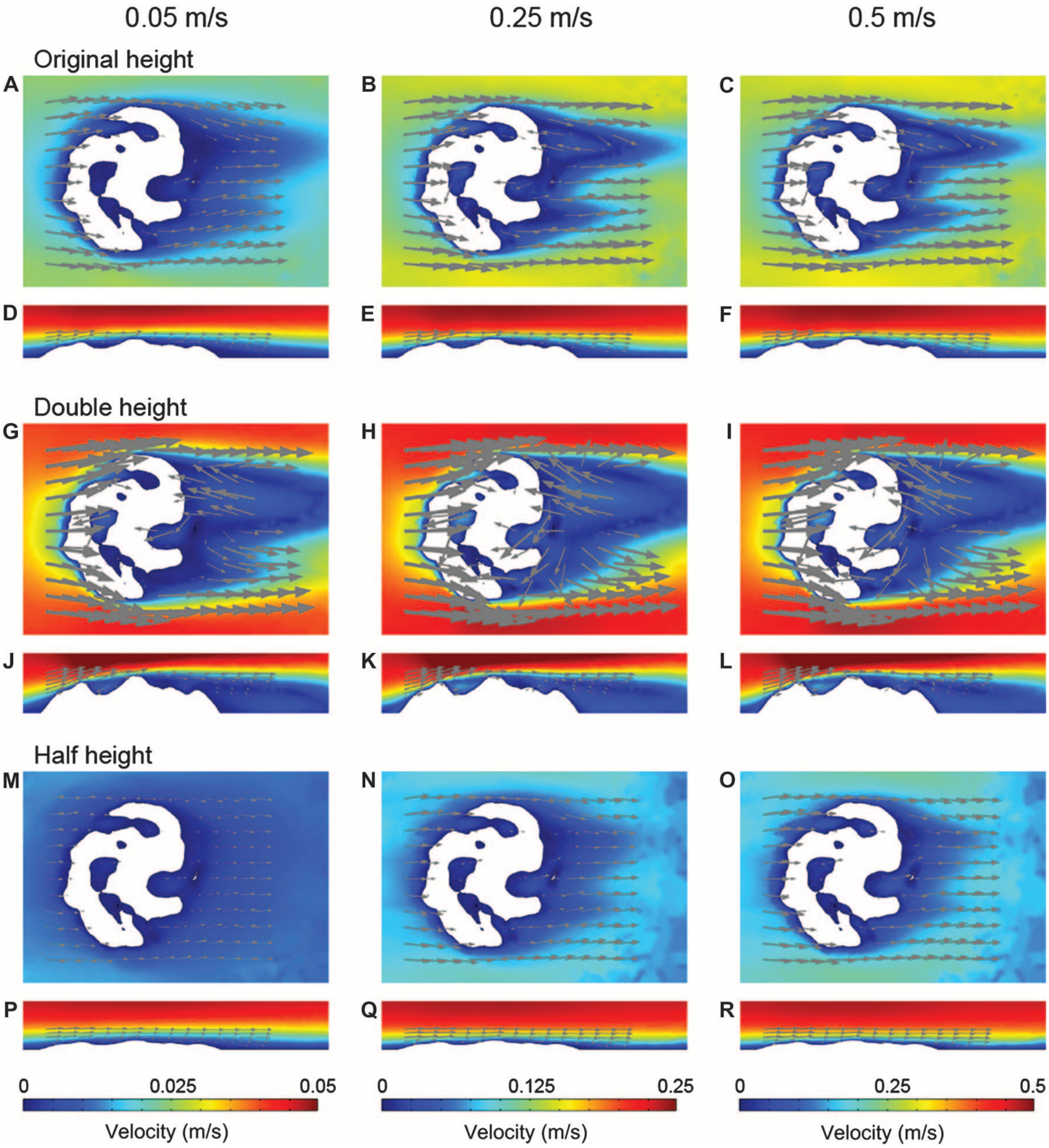

Fig. 3. CFD simulations. (**A** to **R**) Details of water flow around *Tribrachidium* oriented at 0° to the current. Model with original height (A to F), double height (G to I), and half height (M to O). Results visualized as two-dimensional plots of flow velocity magnitude with flow vectors (gray arrows; length of arrows proportional to the natural logarithm of the flow velocity magnitude), in upper (A to C, G to I, and M to O) and lateral (D to F, J to L, and P to R) views. The ambient flow is from left to right.

modulating general flow patterns; the half-height model shows much weaker recirculation in the wake of the organism (and hence weaker flow toward apical pits), whereas the double-height model shows much stronger recirculation, thus reinforcing the results obtained with the original model. Moreover, these results are consistent for all tested current velocities.

Together, the CFD simulations demonstrate that the external surface morphology of *Tribrachidium* generates a distinctive recirculating flow pattern that concentrates flow along the three raised branches and up toward the circular depressions at the apex. Similar flow patterns occur when *Tribrachidium* is placed in different orientations with respect to the current, suggesting that a specific orientation is not critical for controlling the flow of water around the organism or for producing the observed flow patterns. Moreover, this flow pattern is not developed in simulations using the null model, demonstrating that the surface architecture of the organism is essential for creating recirculation. Last, these simulations illustrate that, in the event of any postmortem compaction of fossils, the original uncompacted organism would have produced much stronger recirculation patterns; hence, the flow patterns resulting from our original model should be viewed as conservative.

DISCUSSION

Functional morphology and feeding mode of *Tribrachidium*

The results of the CFD simulations strongly support a suspension-feeding lifestyle for *Tribrachidium*. Rather than distributing flow evenly across the external surface of the organism (as predicted for osmotrophy), flow is slowed and directed by the three primary arms upward toward the apical pits. Our simulations using models with variable relief demonstrate that in the event of any postmortem vertical compaction of fossils, these observed flow patterns would have been stronger and more pronounced in the living organism. Unlike flume studies using models of Ediacaran frondose taxa, where water flow was demonstrated to be slowed and evenly distributed across the entire surface of the frond [thus supporting the inference of osmotrophy (*32*)], our simulations demonstrate that water flow is directed toward localized areas at the top of the organism where small-scale recirculation develops. In generating low-velocity recirculation patterns above a specific part of the organism's anatomy, these results strongly suggest (i) the use of a suspension-feeding strategy for gathering nutrients and, potentially, (ii) the presence of specialized filtering/sieving structures associated with the apical pits. Our null model (that is, an unornamented hemisphere) produced flow patterns that are more compatible with osmotrophy (Fig. 2, M to R, and fig. S5), even though SA/V ratios are minimized with this surface geometry. This suggests a trade-off between overall SA/V ratio (which is increased by folding, crimping, and more complex surface architecture) and the distribution of flow (which is more even around the unornamented null model), indicating that a hemispherical (and nonfractal) body plan may be poorly adapted for osmotrophic feeding.

Extant suspension feeders use a wide variety of different strategies for capturing food (*31*, *32*, *34*, *39*). In the absence of inferring movable filter-feeding structures that are not preserved in *Tribrachidium* fossils [either for active particle capture or for pumping water past a filtering surface (for example, cilia)], the recirculation patterns observed in the CFD analyses of *Tribrachidium* most readily lend themselves to interpretation in terms of passive suspension feeding and a "gravitational settling" strategy for particle capture (*34*, *39*, *40*), whereby particles settle onto a sieving/filtering apparatus under the influence of gravity. This method of food capture is maximized at lower flow velocities and is dependent on the orientation of the particle collector relative to the gravity vector (*31*, *40*). Our CFD simulations suggest that the surface architecture (principally the three primary branches) of *Tribrachidium* may represent an unusual strategy for slowing water flow and creating small-scale recirculation patterns. Within these low-velocity zones above the apex of the organism, larger particles fell out of suspension under the influence of gravity, settling on the collecting apparatus. This method of passive suspension feeding is thought to be important for nutrient acquisition in extant bivalves (*41*) and zooanthids (*34*, *42*).

The sediment-water interface in modern marine settings is typically rich in microbial biomass and larger aggregates of organic matter. This organic matter is easily resuspended by water currents and is likely just as valuable a food resource for suspension feeders as it is for deposit feeders (*40*). In Ediacaran "matground" shallow-water environments, the volume of flocculated and particulate organic matter derived from erosion of mats was likely much higher than it is in modern settings [for example, see Mariotti *et al.* (*43*)], and thus suspension-feeding strategies reliant on gravitational settling were likely feasible.

Sedimentological evidence from fossil beds preserving *Tribrachidium* indicates that ambient currents were either bi- or multidirectional (*20*), which can pose challenges to many extant shallow-water suspension feeders that need to remain oriented normal to the current to feed effectively [for example, gorgoniids (*34*)]. However, our CFD analyses demonstrate that flow patterns around *Tribrachidium* were not significantly affected by orientation to the current, and thus suspension feeding would have been an effective strategy in an environment with variable current directions. Moreover, modeled recirculation is substantially stronger when the ambient velocity is 0.2 m/s or greater (Fig. 2), suggesting that feeding in *Tribrachidium* may have been more efficient in stronger currents. The morphology of *Tribrachidium* lends some support to this interpretation; many sessile organisms in modern shallow-water environments characterized by strong (and either bi- or multidirectional) currents have adopted an approximately hemispherical body plan as an adaptation to minimize drag, and thus prevent themselves from being ripped from the substrate (for example, limpets and barnacles). The secondary branches and "tentacular fringe" may also represent adaptations to life in strong currents; the secondary branches have the effect of roughening the overall hemispherical aspect of the organism, which promotes turbulence close to the surface and prevents the separation of fluids as they travel around the body [thus reducing drag (*34*)]. However, these structures are not sufficiently well preserved on the fossil (and hence not adequately resolved in the three-dimensional model) to fully test this hypothesis. Nevertheless, our CFD analyses and interpretations of functional morphology strongly suggest that *Tribrachidium* was well adapted to shallow-water environments and could have successfully pursued a suspension-feeding lifestyle in both strong and variable current regimes.

Complexity of Ediacaran shallow-marine ecosystems

Ediacaran ecosystems are thought to have been relatively simple, comprising few unique modes of nutrient acquisition and characterized by limited biotic interactions between organisms [the "Garden of Ediacara" (*5*, *44*–*46*)]. The "Cambrian explosion" is thus inferred to have been as much a behavioral and ecological revolution, including the appearance of predation, infaunal deposit feeding, and active filtering, as a rise in metazoan diversity and morphological disparity (*47–49*). Recent compilations restrict Ediacaran organisms' strategies for obtaining nutrients to osmotrophy, saprophagy, and surficial grazing (*5*, *10*), suggesting that these organisms constructed communities with limited trophic complexity and performed only restricted roles as "ecosystem engineers" (*1*, *48*, *49*). Here, we provide quantitative and qualitative evidence to increase the number of known Ediacaran feeding modes to include suspension feeding, which performs a number of vital ecological roles in modern benthic marine ecosystems. This in turn suggests that Ediacaran ecosystems may have been more complex than previously appreciated and that Ediacaran organisms may have performed a role in engineering their environment by removing suspended organic matter from the water column in shallow-marine settings.

Suspension feeding is a critical first link in aquatic food chains (*50*) and plays a vital role in ecosystem maintenance by removing suspended particulate organic matter, thus increasing light penetration and oxygenating the water column (*51*, *52*). Although dissolved organic carbon was likely the dominant nutrient source in deeper-water environments during the Ediacaran period [resulting in communities dominated by macroscopic osmotrophs (*7*, *11*, *25*)], little is known or has been hypothesized about the nature of bioavailable carbon in shallow-water settings. We have demonstrated the existence of probable suspension feeders in fossil communities as old as 555 to 550 Ma from South Australia, Ukraine, and Russia, suggesting that particulate organic matter may have been an important food source in shallow-water Ediacaran paleoenvironments. There is both body fossil and biomarker evidence for a diverse plankton (including a significant eukaryotic component) from the Cryogenian (~750 Ma) onward (*53*), which may have represented an abundant food source for early macroscopic suspension feeders. In addition to this, particulate organic matter resuspended by currents after the erosion of ubiquitous seafloor microbial mats (*43*) may also have been an important source of nutrients.

Establishment of *Tribrachidium* as a probable suspension feeder raises the possibility that other Ediacaran organisms might also have been able to gather nutrients in this fashion. *Tribrachidium* is hypothesized to form part of a larger "clade" termed Triradialomorpha (*1*, *5*), which is founded on the basis of a shared triradial body plan. Other enigmatic taxa within this putative grouping include *Albumares*, *Anfesta*, and *Triforillonia*, although the latter two genera lack the spiral rotation of arm-like structures that is seen in *Tribrachidium*. These other triradialomorphs are typically much smaller than *Tribrachidium* [~8 to 26 mm in diameter; (*20*, *54*)] and would therefore have been situated lower in the boundary layer (and thus been subject to lower current velocities). However, it is conceivable that the surface geometry of these taxa might also have served to manipulate water flow and thereby aided nutrient acquisition (although we note that these taxa appear to lack the apical "pits" that we hypothesize are key to this method of feeding in *Tribrachidium*). More broadly, our results raise the possibility that many other Ediacaran taxa with non-analog body plans may exhibit adaptations to manipulate water currents to aid in feeding. Future work using CFD to analyze flow patterns around other Ediacaran organisms will test this hypothesis.

Two additional aspects of Ediacaran ecosystems that are not addressed in our analyses, but which would likely have had an important effect on patterns of fluid flow near the sediment-water interface, are (i) seafloor microbial mats and (ii) dense epibenthic communities of Ediacaran organisms. Both of these aspects would have aided organisms with osmotrophic feeding and suspension feeding habits. Seafloor microbial mats were critical ecospace modifiers in Ediacaran ecosystems (*3–5*), both in terms of providing a firm substrate for the attachment of epibenthic Ediacaran organisms and as a nutrient source for surficial grazers and saprophytes (*10*, *22*, *23*). Microbial mats would also have added roughness, thus creating turbulent fluid flow immediately above the substrate (*55*, *56*). Likewise, dense communities of relatively low-relief, sessile epibenthic organisms would have broken up the developing boundary layer and guaranteed a consistent flow of suspended (or dissolved) nutrients (*55*). Simulating the effects of both a roughened substrate surface and dense epibenthic communities is not computationally tractable with existing techniques; however, we suggest that these aspects may have had a large influence on hydrodynamic conditions at the sediment-water interface and in structuring Ediacaran benthic communities.

In summary, our CFD analyses demonstrate that the external surface morphology of *Tribrachidium* altered ambient water flow to produce low-velocity circulation above extremely localized areas around the organism, which is consistent with the interpretation of *Tribrachidium* as a suspension feeder rather than as an osmotroph. Specifically, we find that the three primary branches act to slow water flow and direct it up toward the apex of the organism, where small-scale recirculation develops directly above apical pits. This recirculation occurs at a range of simulated current velocities regardless of the organism's orientation to the principal direction of flow. We suggest that this low-velocity zone of recirculation allowed larger particles to fall out of suspension, whereupon they were collected in the apical pits and subsequently metabolized (suspension feeding via "gravitational settling"). This hypothesis suggests that Ediacaran organisms used a larger diversity of feeding strategies than is currently appreciated and that they may have played a role as rudimentary ecosystem engineers, albeit in a fashion that became rare in the Phanerozoic with the disappearance of microbial matgrounds.

MATERIALS AND METHODS

X-ray microtomography

A latex cast of a well-preserved specimen of *T. heraldicum* (020N-033W-TBE) was imaged using x-ray microtomography. The scan was conducted on a SkyScan 1172 in the School of Dentistry at the University of Birmingham, UK, using a current/voltage of 100 μA/100 kV, producing a slice-based data set with a voxel size of 13.5 μm. This data set was digitally reconstructed using SPIERS (www.spiers-software.org), and excess material surrounding the fossil was digitally "cropped" using VGStudio MAX 2.2 (www.volumegraphics.com/en/products/vgstudio-max/basic-functionality/). The digital reconstruction was converted into a NURBS surface using Geomagic Studio (www.geomagic.com) (model S1).

Computational fluid dynamics

Simulations of water flow around the *Tribrachidium* reconstruction were performed using COMSOL Multiphysics (www.comsol.com). The computational domain consisted of a three-dimensional half-cylinder (130 mm in length and 25 mm in diameter) and the *Tribrachidium* reconstruction (25 mm in length, 24 mm in width, and 3 mm in height), which was fixed to the lower surface of the domain (fig. S1). The geometry was meshed using free tetrahedral elements, with different mesh sizes examined to determine the optimal meshing parameters (see fig. S6).

To evaluate the influence of mesh size on the results of the CFD simulations, three different meshes were used in a preliminary examination of mesh quality. These were coarse (maximum element size of 3.57 mm and minimum element size of 1.07 mm), moderate (maximum element size of 2.39 mm and minimum element size of 0.714 mm), and fine (maximum element size of 1.89 mm and minimum element size of 0.357 mm) meshes. In all cases, larger elements were used in regions of the computational domain far away from the fossil, whereas smaller elements were used close to the fossil. Broadly, the same flow structures can be observed for all three meshes (fig. S6). However, the patterns of recirculating flow above the circular depressions are less well developed in the simulations with coarse meshes than they are in those with moderate or fine meshes. This is most pronounced when the ambient velocity is 0.25 m/s or greater (for example, compare flow vectors in fig. S6, F, L, and R). In contrast, the differences between moderate and fine meshes are minor. We therefore selected a moderate mesh for use in our study because the resulting flow patterns are virtually indistinguishable from those of the fine mesh (guaranteeing computational accuracy) and using a moderate mesh enhanced the computational efficiency of the simulations.

An inlet with a normal inflow velocity boundary condition was defined at one end of the half-cylinder, and an outlet with a zero pressure boundary condition was specified at the opposing end. Boundaries at the top and sides of the half-cylinder were "open" (slip boundary condition), approximating flow through the domain, whereas the lower boundary of the semicylinder and the boundaries at the water-fossil interface were "solid" (no-slip boundary condition), fixing the flow velocity at zero.

Three-dimensional, incompressible flow was simulated through the domain, with a stationary solver used to compute the steady-state flow patterns. Ten ambient flow velocities of 0.05 to 0.5 m/s (Reynolds numbers of 1225 to 12250) were simulated, and in all cases, the Reynolds-averaged Navier-Stokes (RANS) equations were solved using the shear stress transport (SST) turbulence model. Simulations were performed with the fossil at three different orientations to the unidirectional current. In addition, simulations were repeated using a smooth unornamented hemisphere (same dimensions as *Tribrachidium*) as a null model. Last, we ran simulations with the height of the original *Tribrachidium* reconstruction both doubled and halved.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/1/10/e1500800/DC1

Fig. S1. Computational domain for CFD simulations.

Fig. S2. Results of CFD simulations with *Tribrachidium* oriented at 0° to the current, visualized as two-dimensional plots of flow velocity magnitude with flow vectors (gray arrows; length of arrows proportional to the natural logarithm of the flow velocity magnitude).

Fig. S3. Results of CFD simulations with *Tribrachidium* oriented at 120° to the current, visualized as two-dimensional plots of flow velocity magnitude with flow vectors (gray arrows; length of arrows proportional to the natural logarithm of the flow velocity magnitude).

Fig. S4. Results of CFD simulations with *Tribrachidium* oriented at 240° to the current, visualized as two-dimensional plots of flow velocity magnitude with flow vectors (gray arrows; length of arrows proportional to the natural logarithm of the flow velocity magnitude).

Fig. S5. Results of CFD simulations with the null model, visualized as two-dimensional plots of flow velocity magnitude with flow vectors (gray arrows; length of arrows proportional to the natural logarithm of the flow velocity magnitude).

Fig. S6. Comparison of the CFD simulations with different mesh sizes, visualized as two-dimensional plots of flow velocity magnitude with flow vectors (gray arrows; length of arrows proportional to the natural logarithm of the flow velocity magnitude).

Model S1. Digital reconstruction of *Tribrachidium* in IGES format.

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Acknowledgments: We thank M. Holder and P. Cooper for assistance with x-ray microtomography, and J. Phillips for advice on CFD. M.L. thanks the Natural Sciences and Engineering Research Council of Canada for generous funding. We are grateful to M. Droser and C. Hall (UC Riverside) for providing the specimen of *Tribrachidium*, for comments on an earlier version of the manuscript, and for making their "in review" article available to us. We would also like to thank L. Tarhan, B. MacGabhann, and an anonymous reviewer for constructive comments that considerably improved an earlier version of the manuscript. **Funding:** I.A.R. was supported by an 1851 Royal Commission Research Fellowship. **Author contributions:** S.A.F.D. and M.L. conceived the study. I.A.R. conducted x-ray microtomography and ran CFD simulations. I.A.R. and R.A.R. carried out three-dimensional computer reconstruction. All authors analyzed the results and wrote the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors and the digital model of *Tribrachidium* will be saved in the online data archive Morphosource.

Submitted 18 June 2015
Accepted 5 October 2015
Published 27 November 2015
10.1126/sciadv.1500800

Citation: I. A. Rahman, S. A. F. Darroch, R. A. Racicot, M. Laflamme, Suspension feeding in the enigmatic Ediacaran organism *Tribrachidium* demonstrates complexity of Neoproterozoic ecosystems. *Sci. Adv.* **1**, e1500800 (2015).

Science Advances

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Imran A. Rahman, Simon A. F. Darroch, Rachel A. Racicot and Marc Laflamme (November 27, 2015)

Sci Adv 2015, 1:.
doi: 10.1126/sciadv.1500800

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