A biomechanical approach to Ediacaran hypotheses: how to weed the Garden of Ediacara
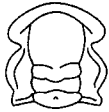
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LETHAIA

Flume experiments and analytical approaches are undertaken to determine the stability of flat-lying Ediacaran organisms in fluid flow. Organisms such as *Dickinsonia* would not have been viable if reconstructed as free-living worms or syncytia. Models of flat-lying Ediacarans occupying a range of densities well beyond those of suggested modern analogs were dislodged by fluid flow taken as typical of Ediacaran paleoenvironments. Analytical tests suggest that parameters such as thickness of the organism and its coefficient of friction have little effect over the range of flows being considered here. These results lead to four non-exclusive interpretations of fossils of flat-lying Ediacarans: (1) The organisms have been transported from a quieter environment (in which case their pristine preservation is similarly puzzling); (2) they had a density approaching that of a flatfish; (3) they were secured to the substrate in some manner; (4) they lived partially or wholly beneath the substrate surface. □*Precambrian, Ediacara, DICKINSONIA, biomechanics, models.*

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Proposing hypotheses for the taxonomic affinity and life habits of Ediacaran organisms has become a perplexing cottage industry (Valentine 1992; Buss & Seilacher 1994; Retallack 1994). In large part, the difficulties associated with identifying those characteristics of the organisms that are familiar aspects of known groups, versus those that are clearly unique to this Precambrian assemblage, have arisen from the unusual combination of soft-bodied preservation in coarse sediment that is the hallmark of the Ediacaran biota. To gain better biological understanding of the Ediacarans, researchers have turned to any means at their disposal, including sedimentological evidence, taphonomic clues, and other synthetic methods.

Leaving aside the debate as to whether or not a single unifying theme should be sought when approaching these organisms, it is easy to recognize that two distinct camps have arisen regarding Ediacaran affinity: those who see convincing evidence in these fossils for a wide range of synapomorphies with known phyla within the Metazoa (Runnegar 1982, 1995; Gehling 1987, 1988, 1991; Jenkins 1992; Glaessner 1984, Waggoner 1996), and those who

deny most of these resemblances and view the Ediacarans as at least representative of new classes or phyla (Fedonkin 1985), if not new modes of organismal construction that merit a new Kingdom (Seilacher 1989, 1992; Gould 1989). The diverging general conclusions of these researchers are based on numerous examinations of Ediacaran morphology and/or taphonomy (often of the same specimens!), but to date most experimental or actualistic testing has pursued questions of preservation (Norris 1989; Retallack 1994), while exploring possible Ediacaran life modes has remained a rarity (Runnegar 1982).

We believe that a more systematic approach towards examining the mechanical properties of these organisms may allow researchers to limit the many proposed affinities (from jellyfish to lichens) for Ediacaran organisms. This paper explores one such approach and is meant as a proposal and demonstration of methodology. The results presented here for one subset of Ediacaran organisms (*Dickinsonia*-like flat-lying forms) are preliminary. However, the approach should be generalizable to analyses of many of the more contentious members of the biota.

A case study

The rift in deducing Ediacaran affinities is well illustrated by the interpretation of flat-lying forms such as *Dickinsonia*. Two of the most discussed hypotheses for *Dickinsonia* are its interpretation as a mobile, muscular, surface-dwelling flattened annelid worm (Runnegar 1982; while other flattened forms like *Phyllozoon* are seen as having features setting them apart, perhaps as 'metaphytes', Runnegar 1995) and the alternative interpretation that unites *Dickinsonia* with forms such as *Pteridinium* and *Phyllozoon* as members of a group of quilted, flattened, hydrostatically stiffened organisms (Seilacher 1989) lacking obvious internal or external organs (Seilacher 1984).

Importantly, different predictions about the behavior of a flat Ediacaran under fluid flow can be made depending on the taxonomic affinity (and hence life mode) one proposes. A flat, surface-dwelling muscular worm should be more resistant to the effects of hydrodynamic lift than a less dense alternative, such as a syncytial quilted organism (i.e. a 'flat-recliner' of Seilacher 1994). Likewise, a flat Ediacaran lying beneath or within the sediment should be relatively resistant to the problems of stability in fluid flow. Restated, if seen as a mobile worm, *Dickinsonia* should have characteristics much like proposed modern analogues: (1) muscles which imply mobility (and perhaps the possibility of leaving trace fossils), a dependence on oxygen, and a body density close to that of other muscular marine invertebrates, and (2) a life near the surface of the substrate. A dickinsonid with a quilted construction opens up a number of different avenues for reconstructing these organisms: (1) They probably were not self-locomotory, (2) they need not to have been limited to environments where oxygen was present (i.e. the sediment surface), and (3) their density is uncertain but likely to be less than that of a muscular worm of similar proportions, and most probably closer to that of seawater (particularly if their proposed syncytial affinities are considered; Seilacher 1989, 1994).

The ability of researchers to further such inferences has been founded on their individual insights into extracting clues about body toughness, environmental tolerances, preservation potential, and the cohesiveness of the Ediacaran biota as a single morphogenetic/systematic unit. We propose that modelling and analytic approaches to these questions might be an underutilized tool with which to constrain some aspects of the biology and taxonomic affinities of Ediacaran organisms. Given an organism of known density, we can document the range of stability that corresponds to the current velocities it would have been able to withstand without being dislodged from the substrate. This approaches the type of data called for by Palmer (1996) when trying to reconcile the burial of 'Ediacaran jellyfish' in density currents. From the information gained by repeating the experiment for organisms of different densities, one should be able to address questions about the feasibility of various life-mode and body construction combinations when placed within the context of Ediacaran current regimes.

Experimental procedures

Parameters

Models of elliptical, flat-lying Ediacarans were produced using several approaches. An intermediate-sized organism was chosen as the theoretical template for these models, which measure approximately 13 cm in length, 8.5 cm in width, and 0.6 cm in thickness at the center, tapering slightly towards the periphery. These dimensions are in accordance with those of *Dickinsonia* (Wade 1972; Runnegar 1982), thickness being the most difficult dimension to gauge from fossils (Runnegar quotes thickness ranging from 0.1 to 0.6 cm and from 0.4 to 2.4 cm upon contraction for a 1 m long *Dickinsonia*). Choosing a thickness near the upper range of the unconstrained value is actually conservative in this context, as will be discussed below.

We began with a Kapak–Scotchpak pouch sealer and heat-sealable plastic pouches. Shaped pouches were filled with various concentrations of Karo syrup (density=1.2 g/cm^3), water (density=1.0 g/cm^3), sand (2.7 g/cm^3) and sealed. In this manner a fairly consistent model shape was achieved, while density was allowed to vary over a range corresponding to a number of naturally occurring substances.

A second set of models were cast from a latex-like material (Polygel40; density 1.0 g/cm^3; produced by Polytek). By mixing various amounts of sand with Polygel40, models spanning a range of densities were produced. These had several advantages over those made using the Kapak–Scotchpak pouches: they were essentially invariant in size and shape, all having been cast from the same mold (the pouch models varied more in size and shape), they lacked the stiffened seams that were inescapable using the heat-sealing method, and the components were much more manageable. The constructional materials for both sets of models produced the pliant, yet tough, integument hypothesized for many Ediacarans (Norris 1989; Seilacher 1989).

A flexible and smooth exterior was a side-product of the materials used. Because the surfaces of Ediacaran fossils are demonstrably not smooth, a final set of models was produced using a sculpted reconstruction of *Dickinsonia* with the same dimensions as the other models (Fig. 1). Polygel40 and sand were again used to obtain a range of densities for these models.

All models were 'noncommittal' in the sense that all their aforementioned physical properties resulted from reproducing the direct observations of fossils rather than
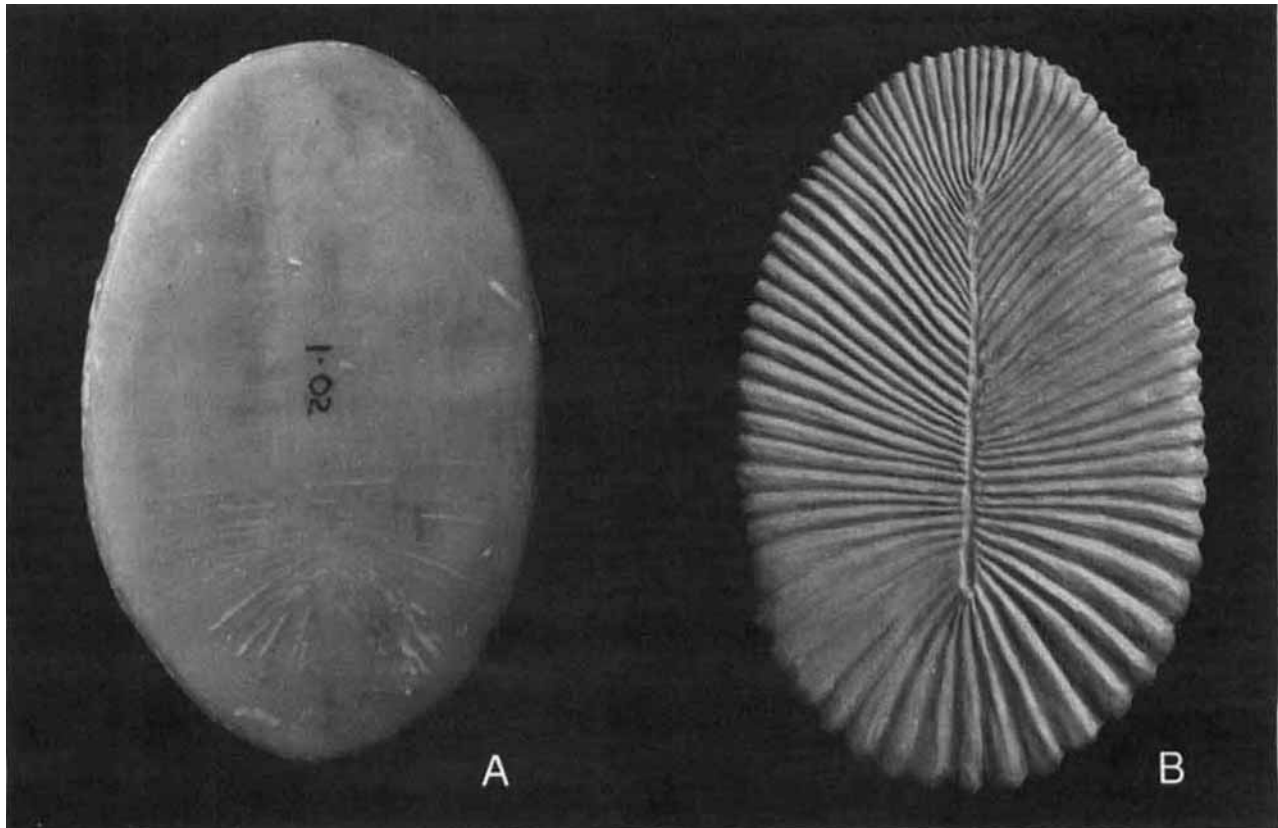
Fig. 1. Photographs of the smooth (A) and sculpted (B) Polygel40 models. Models measure approximately 13 cm in length, 8.5 cm in width, and 0.6 cm in thickness at the midline.

incorporating *a priori* taxonomic interpretations. We thus avoid the circularity of assuming taxonomic affinity so that this affinity may be studied (this assumption necessarily accompanies the inclusion of such problematic taxa in a cladistic analysis; e.g., the inclusion of the Ediacaran *Spriggina* in an analysis of the Arthropoda becomes possible only if one decides beforehand that its ambiguous morphology includes a head and legs homologous to those of arthropods; see Waggoner 1996).

As straightforward as creating model flat-lying Ediacarans is, determining the current velocity at Ediacara is a much more complicated problem. Here we use two methods, both of which we believe provide conservative estimates of the Ediacaran flow regime. Taking the sand in which these fossils are preserved as indicative of the flow velocity under which they lived (a point explored in the conclusions) one may use the grain size, about 0.2 mm (recorded from museum specimens), and associated bedforms to approximate these velocity values. Based on Hjulström's curve (Hsü 1989), these sands would have been eroded at velocities exceeding 20–45 cm/s.

Likewise, associated bedforms in the shape of ripple marks and current ripples with wavelengths ranging from 5 to 17 cm have been reported from the 'fossiliferous hori-

zon – Unit B' at Ediacara (Goldring & Curnow 1967), although the relation of these structures to the fossil-bearing layers themselves was openly questioned by these authors (A. Seilacher adds that he has seen no such structures associated with fossil-bearing layers at Ediacara, personal communication, 1994). Nonetheless, such bedforms have been experimentally produced at a minimum flow velocity of 20 cm/s (range approximately 20–45 cm/s for quartz grains of 0.2 mm; Harms *et al.* 1982). It seems *self-evident, even without the flume results reported here,* that if velocities at Ediacara were high enough to cause sediment transport and bedform formation, a flat-lying organism would have been buried or swept away. Indeed, Goldring & Curnow (1967, p. 208) attributed Ediacaran preservation to the 'rapid smothering of the surface either by the advance of ripples, or more frequently, by vertical accretion of sand'. Again, lacking *in situ* bedforms co-occurring with fossils, flow velocity data are tenuous at best (in the very same paper, these authors propose a window of generally decreased flow energy for the period of most Ediacaran preservation; Goldring & Curnow 1967).

More convincing indications of flow velocity, at least qualitatively, are erosional structures (Goldring & Curnow 1967) and Ediacaran 'drag-marks' (Seilacher

1989). Although not common, both small (truncation sets of up to 5 cm thick) and large (several meters in cross-section) erosional structures have been observed. While the rarity of such structures argues against them having been a major component of the sedimentological setting, the fact that some cores (E3 and E4 of Goldring & Curnow 1967) do display common scour-and-fill structures is further evidence for at least episodic flow velocities capable of moving the accumulating sediment. This corroborates the inferences drawn from Hjulström's curve. The fact that fossils are not found on the soles of the beds bearing scour-and-fill structures (Goldring & Curnow 1967) may indicate that the flow velocities these organisms were capable of withstanding were lower than those responsible for creating the structures.

The most concrete evidence that fluid flows were capable of destabilizing Ediacarans (regardless of their taxonomic affinity) are occasionally preserved 'drag-marks'. These were left as impressions in the sediment as organisms were dragged over the surface of the substrate (Seilacher 1989, Figs. 2, 3). This is clear proof that fluid flow was capable of moving the flat-lying organisms, at least on occasion. With this possibility firmly established, we may pool the various lines of evidence to ground our experiments.

Caveats stated, the minimum consensus value for flow velocity from grain size and associated bedforms is 20 cm/s. We assume that Ediacarans could have remained stable on the substrate at this and lower velocities.

Flume experiments

Once the Ediacaran models were constructed and the general flow regime established, an initial sensitivity test was carried out in a standard recirculating flume to ascertain whether or not the values indicated were near critical. Runnegar (1982) approximated the specific gravity of his reconstructed *Dickinsonia* as 1.0 g/cm^3 based on studies of molluscan 'meat' (Pregenzer 1981). This would make the Ediacarans neutrally buoyant, or very nearly so. We found that all three types of model Ediacarans (pouch, smooth Polygel40, and sculpted Polygel40) of this density were easily dislodged at flow velocities lower than 10 cm/s, i.e. a much lower velocity than we have assumed was common. It was thus determined that further experiments were justified.

Flume experiments were undertaken in a recirculating flow tank (Vogel & LaBarbera 1978). A water depth of approximately 20 cm was maintained in the working section throughout the experiments. This relatively low water level enabled higher flow velocities to be reached and the behavior of the models to be tested under a wider spectrum of conditions. Laminar flow could be maintained up to flow velocities of approximately 40 cm/s. Speeds were calibrated using fluorescence dye in free

stream and a stop watch. The dimensions of the flume, especially its width, are critical to these types of experiments, as they determine the size of the boundary layer in which a velocity gradient is developed. In this case, the width of the tank (20 cm) is over twice the width of the model (8.5 cm), and this creates the possibility that the model will experience an across-tank velocity gradient. However, across-tank velocity profiles taken up to free-stream velocities of 40 cm/s revealed that for the middle 10 cm of the tank's working section a velocity gradient is not detectable.

The choice of experimental substrate was complicated by differing interpretations of the natural environment of these fossil organisms. The literature varies widely in opinion concerning the environment of deposition for the organisms found at Ediacara, Australia. What some authors see as a normal, well-aerated, marine deposit (Goldring & Curnow 1967; Seilacher 1989), others see as a beach or lagoonal setting (Jenkins *et al.* 1983). Obviously, these differing views would affect interpretations regarding current velocities, amount of transport prior to preservation, and the grainsize of the sediment upon which the organisms lived. As a first pass, a range of sediment types was used that might encompass most possibilities. Experiments were carried out on a fine sand substrate, the smooth plexiglass surface of the tank bottom itself, and, for the Kapak–Scotchpak models, on a firmer clay bottom (industrial grade kaolinite prepared as per J. Southard, personal communication, 1994).

Each model organism was oriented with its long axis parallel to the flow direction in the center of the tank's working section before flow was initiated. Experiments showed this to be the most stable orientation. Flow velocities were then gradually increased by fixed intervals of approximately 5 cm/s. After each increase the behavior of the model (and sediment) was observed for 1–2 min to characterize its stability under this flow velocity. Flow velocity was increased until the model became dislodged and traveled downstream. We have not separated U_S (slip-speed) and U_L (liftoff speed), as defined by Arnold & Weihs (1978). In practice, the two were difficult to distinguish in these experiments; and we use the term 'slip-speed' for the speed at which dislodgement occurred from a stationary spot (by either traction or lift).

In addition, for the Kapak–Scotchpak models three different model–sediment interfaces were explored. Models were tested on the surface of a flat substrate, in a depression that accommodated approximately half their thickness, and in a deeper depression that made the models flush with the sediment surface. The results of these last two cases proved to be identical and are mentioned in the conclusion; those for flat substrates proved consistent with those for the Polygel40 models reported in detail. Also, because of the constraints of working materials, these additional positionings were only carried out using

the sand substrate (adjustments to the clay turned out to be infeasible, and carving into the plexiglass was out of the question). We believe the results from the sandy bottom to be generalizable, although, as might have been expected given the cohesive nature of clay, most models seemed to have a slightly higher slip speed on the clay substrate than flat sand or plexiglass (on the order of 5–10 cm/s). The fact that the clay substrate was quickly eroded at these experimental speeds (runs often ending due to the opaqueness of the flow tank's water), however, calls into question whether this combination of current velocity and sediment size should be considered, since it is probably only ephemeral outside of the laboratory.

Results

Executing repeated runs allowed us to determine the range of slip speeds for models of different densities, construction materials, and surface textures (Fig. 2). These results suggest that slip speed is strongly dependent on model density and somewhat dependent on surface texture, but the effect of substrate is more complicated. For example, slip speed always increased for denser models, and smooth models had a higher slip speed than textured models, but the effect of substrate was not as predictable:
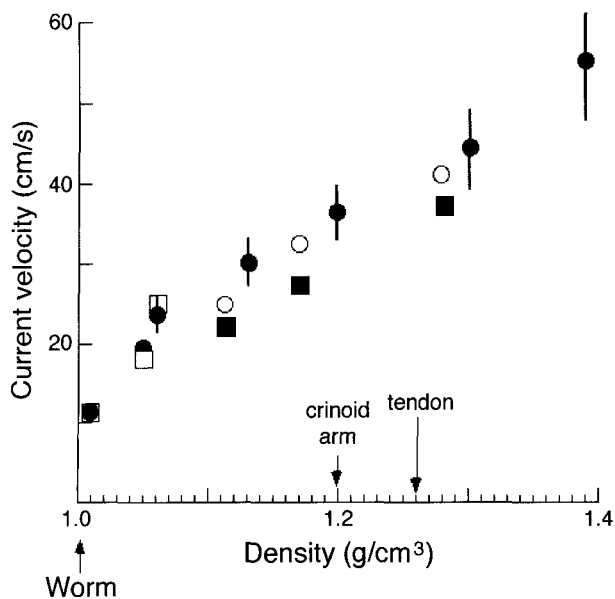

Fig. 2. Results of the flow tank experiments for the Polygel40 models. (Results for the Kapak–Scotchpak models are discussed in the text.) Solid circles: smooth models on plexiglass; open squares: smooth models on sand; open circles: sculpted models on plexiglass; solid squares: sculpted models on sand. For clarity, only error bars for smooth models shown; these represent ±1 standard deviation. The densities of a worm (Runnegar 1982), crinoid arm (Baumiller 1992), and tendon (Wainwright *et al.* 1976) are plotted for comparison.
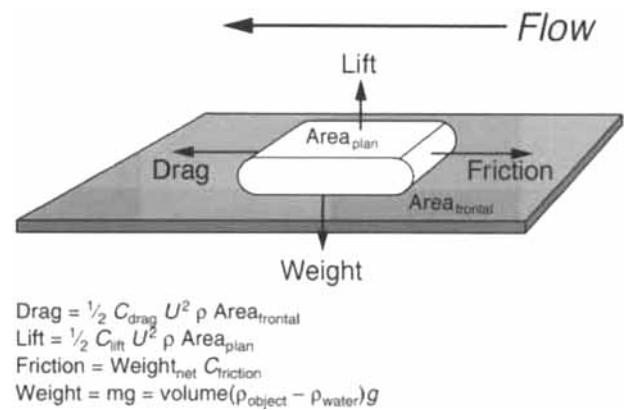

Fig. 3. A schematic representing the forces acting on a submerged object resting on the substrate in unidirectional flow.

$$Drag = \tfrac{1}{2}\, C_{drag}\, U^2\, \rho\, Area_{frontal}$$
$$Lift = \tfrac{1}{2}\, C_{lift}\, U^2\, \rho\, Area_{plan}$$
$$Friction = Weight_{net}\, C_{friction}$$
$$Weight = mg = volume(\rho_{object} - \rho_{water})g$$

for smooth, low-density (<1.10 g/cm³) models, substrate appeared to have no effect, whereas for models of higher density (>1.10 g/cm³) with a textured surface, the slip speed was lower for sand than for plexiglass.

However, regardless of the substrate or texture, a general conclusion can be drawn from these results: models with densities below 1.10 g/cm³ are unstable at velocities below 25 cm/s regardless of material, substrate and surface texture; while models with densities below 1.05 g/cm³ begin slipping at velocities of 20 cm/s and lower. To be stable at 20 cm/s, a model must have a density much closer to that of a flatfish (density=1.07 g/cm³; Arnold & Weihs 1978) than a worm (density=1.0 g/cm³; Runnegar 1982).

Analytical approach

The experimental results showed that stability may have been a problem for Ediacaran organisms unless their densities approached that of a flatfish. However, because our estimates of their density and texture – and, to a lesser extent, their thickness – are poorly constrained, it would be worthwhile to examine how other changes in these parameters would affect slip-speed. It might then be possible to delimit those combinations of characters that would disrupt stability in 20 cm/s currents. In order to do this, it would be possible, but laborious, to make many more models and test them under different conditions. It is much more practical to approach this problem analytically. Below we will do this following a methodology outlined by Arnold & Weihs (1978).

As shown in Fig. 3, four forces act on a body submerged in a fluid and resting on the substrate. In the horizontal plane, these are: *drag*, acting in the direction of the flow, and *friction*, acting between the model and the substrate, which works in a direction opposite to that of drag. In the
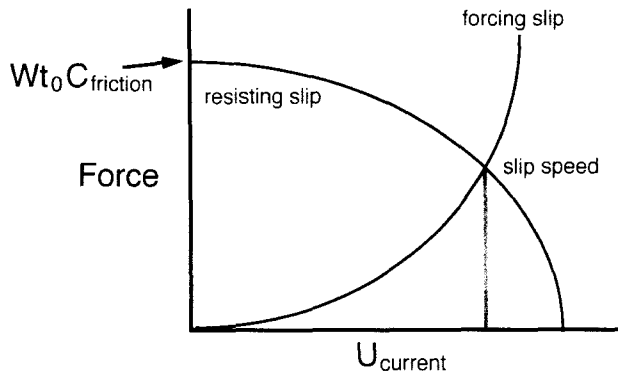
Fig. 4. The interaction of forces as a function of current velocity experienced by an object in Fig. 3. The forces resisting slip decrease with increasing velocity because, as lift increases, the effective weight and thus the force of friction decrease. The forces causing slip increase because of the increase in drag.

vertical plane, the two forces are: *lift*, a force acting perpendicular to flow direction, and *gravity*. Friction is proportional to the model's effective *weight*; *lift* might reduce this effective weight from the actual weight due to gravity.

The forces of drag and lift are proportional to the object's size and shape and are strongly dependent on the current velocity. As flow velocity increases, lift and drag increase. The increase in lift decreases the effective weight, which in turn reduces the force of friction. The onset of slip occurs when the drag force (D) equals the force of friction (F_f) (Fig. 4: a schematic of the two intersecting lines):

$$D=F_f=C_f\,(m_0\,g-L) \qquad\qquad 1$$

where C_f is the coefficient of friction, m_0 is the mass of the object in water, g is the gravitational acceleration, and L is the lift. Drag and lift can be expressed as:

$$D=0.5\,\rho_w\,A_f\,U^2\,C_d \qquad\qquad 2$$

$$L=0.5\,\rho_w\,A_p\,U^2\,C_l \qquad\qquad 3$$

where ρ_w is the density of water, A_f is the frontal area, A_p is the plan area, U is the velocity, C_d is the coefficient of drag and C_l is the coefficient of lift.

Given an object of known dimensions and a fluid of known properties, it should be possible to examine the exact relationship between slip-speed and density if C_f, C_l, and C_d were known. For a given object, these can be obtained empirically.

To obtain C_f, models were placed on a flat plexiglass plate submerged in water, and the slope of the plate was increased until the model started slipping downslope. The tangent of the angle between the plate and the horizontal is defined as C_f. To determine how C_f varies as a function of surface smoothness, materials of different textures were used to cover the surface of the model and of the plexiglass plate.

Although C_d and C_l may be obtained directly by measuring lift and drag for objects of given shapes and sizes, it is also possible to obtain these values from data on slip speeds. This can be done by manipulating equations 1, 2, and 3 such that

$$(2\,m_0\,g\,/\,\rho_w\,U^2)=C_d A_f/C_f+ C_l A_p \qquad\qquad 4$$

By experimentally obtaining the slip-speed for a model with a known C_f, equation 4 can be expressed in terms of C_d and C_l, since all other parameters are known. Repeating the experiment for another model differing from the first only in its C_f value provides a second equation with the same unknowns, C_d and C_l. The two equations can now be solved simultaneously to obtain values of C_d and C_l.

The above strategy was used with two models, each having a density of 1.30 g/cm^3 but one with a C_f of 0.16 and the other with a C_f of 0.36. Using their known dimensions and fluid properties, the equations were solved for C_d and C_l; the values obtained were 0.24 and 0.15 respectively.

Measurements of drag and lift on a stiff clay model mounted on a sting allowed C_d and C_l to be obtained directly; these values, 0.25 and 0.15 respectively, are nearly identical to those from the indirect method and
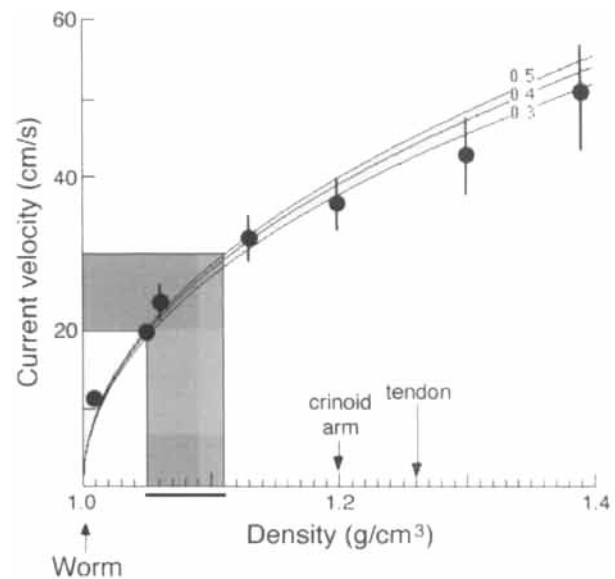

Fig. 5. Results of the flow-tank experiments for the smooth Polygel40 models on plexiglass (same as in Fig. 1). The coefficient of friction for these models is 0.35 ±0.05. The three lines represent the analytical solution for the models assuming three different values for the coefficient of friction (0.3, 0.4, 0.5), a coefficient of lift of 0.15, a coefficient of drag of 0.25, a thickness of 0.6 cm, a length of 13 cm, and a width of 8.5 cm. Note that the solutions are relatively insensitive to the coefficient of friction. The densities of a worm, crinoid arm, and tendon are plotted for comparison. The solid bar along the 'density' axis corresponds to the densities that would have made Ediacarans stable at current velocities between 20 and 30 cm/s.
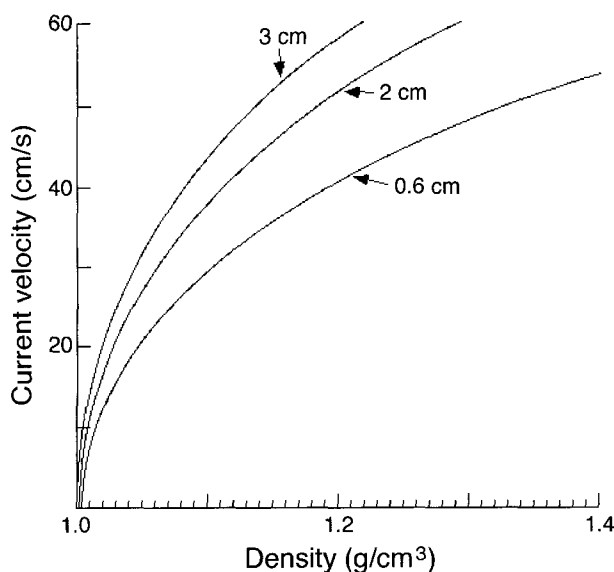
Fig. 6. Effect of size on slip speed. The lines represent analytical solutions for three models similar in every respect to those in Fig. 5 except having a coefficient of friction of 0.3 and different thicknesses (0.6, 2, and 3 cm).

give us some confidence in these values. The latter values were used in the analytical solution.

Given the values of C_d and C_l, the relative stability of the flat-lying Ediacaran could be explored analytically by modifying the values of the relevant and poorly constrained variables such as density and surface texture.

Assuming that the Ediacaran organisms were stable at velocities of 20 cm/s and lower, their density would have to have been in excess of 1.05 g/cm³ (Fig. 5). Note that at low densities this result is insensitive to, and thus independent of, the coefficient of friction (surface texture); this is consistent with the results obtained for the different models. Stability at higher velocities would have required higher densities; for example, if we accept 30 cm/s as the stability threshold, the corresponding density would have to exceed 1.11 g/cm³.

We may also ask what the effect of thickness might have been on stability. In exploring this analytically, we will retain the C_d and C_l values derived empirically for a 0.6 cm thick model, noting, however, that because these values are sensitive to shape they are rough approximations only. As Fig. 6 demonstrates, the effect of thickness on stability can be quite dramatic, and the thicker the object the more stable it tends to be. The reason for this is simple: the mass of an object increases faster than the drag force as the object gets thicker. If we assume that Ediacarans were 2 cm thick and stable at 20 cm/s, they would have had to have a density higher than 1.03 g/cm³, while a 0.6 cm thickness would have necessitated a density of 1.05 g/cm³ or higher. As mentioned at the outset, the chosen model thickness of 0.6 cm is actually at the upper range of

published reports for fossil organisms of this type, and it seems unlikely that *Dickinsonia* was 2 cm thick. A density of 1.05 g/cm³ thus appears to be the minimum for a free-living Ediacaran stable in currents of up to 20 cm/s.

Conclusions

'As such the vendozoan model is rendered immune to actualistic analysis. If they represent a failed evolutionary experiment, using a unique approach to the problems of organismic functioning, and entirely without surviving descendants, then there is no way of exploring the feasibility of the model.' (Gehling 1991, p. 193.)

Contrary to this sentiment, which reflects the plethora of ideas about Ediacarans that seem 'surprisingly difficult to falsify' (Retallack 1992, p. A226), we believe that there may be methods by which the range of the biologically possible can be limited to the physically plausible (see also Runnegar, 1995). At the very least we have demonstrated in this preliminary analysis that a flat-lying, unsecured Ediacaran of the density of a worm could not have lived at the surface of the Ediacaran substrate. Our specific conclusions are clearly contingent on the environment in which these organisms were living, but the methods outlined here and general relationship between density and slip-speed (Fig. 5) are applicable to tests of other Ediacaran hypotheses.

Our flow-tank experiments suggest that for Ediacarans to have been free-living and stable at currents of 20 cm/s, a density in excess of 1.05 g/cm³ would have been required. Our analytical approach allows us to test the sensitivity of these results with respect to parameters such as friction and thickness. There appear to be four basic ways to reconcile these results with the two established schools of thought about forms such as *Dickinsonia*:

1 The fossils may not have been preserved *in situ*, and 20 cm/s currents are in excess of the conditions typically experienced by these organisms. In other words, we have undertaken our experiments at too high a flow velocity because these organisms normally lived in quieter environments. As previously mentioned, there is some independent evidence for such transport in the drag marks documented by Seilacher (1989) which indicate movement of these organisms by fluid flow, as well as reports from other parts of the world of similar forms preserved in much finer sediments (e.g., Narbonne *et al.* 1994). Additionally, many of these forms are thought to have lived on fine clays and were preserved by burial under storm beds or turbidites (see Narbonne 1998). Even so, this implies that the organisms encountered flow velocities on the order of our conservative estimate at least once. The apparent stability of these organisms inferred from their

flat and ubiquitous pristine preservation thus seems just as puzzling in light of our results, in addition to surviving the 'submarine equivalent of a washing machine full of sand' (Palmer 1996, p.114) which such preservation entails.

2   The organisms may have been more dense than expected. They would have needed to be nearly as dense as a flatfish, which would seem to contradict previously hypothesized scenarios (flattened worms and syncytia). It remains unclear what this option might mean for lichens (density of wood varies from 0.25 to 1.25 g/cm^3, with an average value of 0.6; Wainwright *et al.* 1976).

3   The organisms might have been secured to the substrate in a manner granting them a very high coefficient of friction. Might *in situ* growth have granted these organisms sufficient purchase on the substrate through the gradual replication of, and continual contact with, the underlying sediment? Could the preponderance of observations of 'biomats' associated with these fossils (Gehling 1986; Fedonkin 1994) serve as a sort of Precambrian fly paper? Or could lichens have been rooted by rhizines?

4   The organisms might have lived partially buried. Our findings may be related to Wade's (1968) observation that the preservation of 'nonresistant' (medusoids) and 'resistant' Ediacaran organisms (e.g., *Dickinsonia*) is indicative of two distinct processes. While Wade assumed that the separation was taphonomic, it may in fact have been ecologic – with at least some proportion of the 'resistant' biota living in closer association with the sediment. In our experiments even the least dense models, if partially buried or placed in depressions in the sand such that they were flush with the sediment surface, were stable in very high flow velocities (in excess of 40 cm/s). This lends increased significance to McMenamin's (1994) experiments that showed sunlight capable of supporting photo-symbionts could penetrate the sandy substrate up to 23 mm. Of course, one must then ask how such organisms came to be buried. *Dickinsonia* preceded the origin of peristaltic burrowing (Runnegar 1982). Although subsequent finds have extended the geologic range of trace fossils indicative of such activities back in time (Runnegar 1994; Seilacher 1994; attributed to nonfossilized metazoans), flat-lying Ediacarans are still commonly interpreted as non-locomotory (Seilacher 1994).

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Cambrian bivalved arthropods

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Siveter, D.J. & Williams, M. 1997: Cambrian bradoriid and phosphatocopid arthropods of North America. *Special Paper in Palaeontology 57*. 69 pp. The Palaeontological Association, London. ISBN 0-901-702-61-7. £30.00 ($60.00).

This monograph is part of a series of publications by the two authors and their collaborators (Williams *et al.* 1994; Hou *et al.* 1996; Melnikova *et al.* 1997; Williams & Siveter, *in press*) aiming toward a comprehensive inventory of an important component of the Palaeozoic arthropod fauna: the bradoriids and the phosphatocopids. These two groups of small bivalved arthropods occur worldwide from the early Cambrian to the early Ordovician. From the time of their discovery in the late 19th century, these fossils were referred to the ostracod crustaceans until their soft parts were discovered in the Upper Cambrian of Sweden (phosphatocopids of the *orsten* faunal assemblage; Müller 1979, 1982), the Middle Cambrian of Australia (Walossek *et al.* 1993), the Lower Cambrian of Great Britain (a phosphatocopid baby, Hinz 1983), and the early Cambrian of China (Chengjiang fauna; Hou *et al.* 1996 for the bra-

doriid *Kunmingella*). These recent discoveries revealed that bradoriids and phosphatocopids had body plans fundamentally different from those of Recent and fossil ostracodes, most of them (e.g., the phosphatocopids) being thought to represent advanced stem-group crustaceans (Walossek & Müller 1992).

The debate concerning the affinity of phosphatocopids and bradoriids, however, is not the focus of Siveter & William's paper. They have produced a much needed classical descriptive treatment of the two groups based on the morphology of the head shields (traditionally termed 'carapaces') in North American faunas. The authors have restudied an impressive amount of material housed in American and European institutions and have also made extensive new collections of the faunas originally described by Matthew (e.g., 1886) in New Brunswick and Nova Scotia more than a hundred years ago. Palaeogeographically, these faunas come from two broad areas: Avalonia (New Brunswick, Nova Scotia, East Newfoundland) and Laurentia (West Newfoundland, Vermont, New York State, Pennsylvania, Tennessee, Oklahoma, Texas, Mexico, Wyoming, Utah, Arizona, British Columbia, Alberta and North Greenland). Stratigraphically, they cover most of the Cambrian Series.