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Segmentation and Oxygen Diffusion in the Ediacaran *Dickinsonia*: an Applied Analysis

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Abstract

Many Ediacarans are constructed of multiple parallel segments. Two forms of segment were analysed in the present study, a cylindrical and cuboidal form. The theoretical surface area to volume (A/V) ratio of a structure composed of cylindrical segments is twice that of one composed of cuboidal segments of the same thickness. In this analysis the Ediacaran *Dickinsonia* was assumed to be a bottom-dwelling marine animal. Individual A/V ratios were calculated for 60 fossil specimens of *Dickinsonia* of known thickness and diameter assuming either a structure composed of tapering cylinders (conical frusta) or tapering cuboids (square frusta). With increasing body diameter a lower limit of the A/V ratio was approached in both structural forms at a body diameter of approximately 50 millimetres. The segments were assumed to contain solid connective tissue. The theoretical oxygen concentration gradient due to simple diffusion into both forms was calculated and the effect of a collagenous segmental wall on these gradients was determined. The cylindrical form with a collagenous wall was found to be viable within the constraints of this analysis but not the cuboidal form. The findings support the hypothesis that *Dickinsonia* could have obtained adequate oxygenation by simple diffusion with cylindrical but not cuboidal segments.

Keywords *Dickinsonia*, Ediacarans, segmentation, oxygen diffusion.

Introduction

In 1964 Berkner and Marshall hypothesised that the trigger for the emergence of metazoans was the appearance of oxygen in the atmosphere. Since then the estimated oxygen content of the Precambrian atmosphere has progressively increased (Butterfield, 2009; Canfield, 2007; Shields-Zhou, 2011), which raises once more the vexed question of the relationship between the structure and the mode of oxygen delivery in the Ediacaran biota (Raff, 1970; Runnegar, 1982).

The characteristic surface feature of many species of Ediacaran is a repeated parallel segmentation. In 1989 Seilacher suggested that a wide range of Ediacarans including *Pteridinium* and *Dickinsonia* had a common structural form composed of parallel chambers underlying the defining surface segmentation (Figs. 1, 2 and 3). He represented these chambers as essentially cuboidal in shape. Grazhdankin (2002) drew these chambers as purely box-like or cuboidal in form with square cross section.

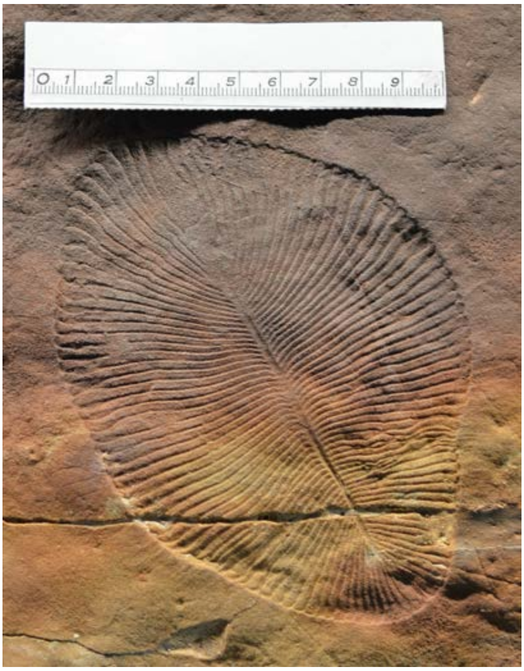

Figure 1: Fossil of Dickinsonia. Scale in centimetres (South Australian Museum, specimen No. P49355).

Figure 2: Fossil of Pteridinium. Scale in centimetres (specimen by courtesy of Dr Jim Gehling, South Australian Museum).

The surface area to volume (A/V) ratio is critical for the survival of marine organisms that are dependent solely on the diffusion of oxygen from a watery environment through their surface and into their living tissue (Krogh, 1941; Alexander, 1971). Laflamme (2009) modelled *Pteridinium* on the basis of a cuboidal structure in order to analyse the A/V ratio. However illustrative material presented by Jenkins (1992) raised the possibility that the segments in *Pteridinium* may have been more cylindrical than cuboidal in shape and recent photographic evidence lends further support to this concept (Elliott, 2011).

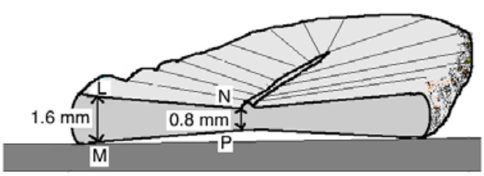

Figure 3: Schematic diagram of Dickinsonia lying on the biomat covering the ocean floor (dark grey shaded area) showing a section through a tapering cylindrical segment and diffusion paths LM of thickness 1.6 mm adjacent to the periphery and NP of thickness 0.8 mm adjacent to the midline.

Recently Retallack (2012) has suggested that some Ediacarans including *Pteridinium* and *Dickinsonia* were terrestrial organisms similar to lichens. Though the matter is clearly contentious, it would appear that the generally held view at the present time is that the Ediacarans were marine organisms (Switek, 2012) and for the purposes of the present palaeo-physiological analysis the author has assumed that to be the case.

The first objective of the present study was to analyse theoretically the A/V ratio of two hypothetical structural forms, one composed of purely cylindrical segments and the other of purely cuboidal segments. These ratios were then applied to data from actual fossil specimens of *Dickinsonia* in which the profile thickness and diameter were known. In this way the A/V ratio of each specimen could be calculated for either a purely cylindrical or cuboidal form of segmentation and compared. Finally. the theoretical oxygen concentration gradient in cylindrical and cuboidal segments was calculated and considered in relation to the possible viability of each structural form.

Methods

Factors affecting the A/V ratio

Ratio of diametrical length to arc length

Consider a section composed of *n* semicircular arcs, then

$$l_a/l_d = n.\,\pi.\,r/\,n.2.\,r = \pi/2 \qquad (1)$$

where l_a is the total arc length of the section, l_d is the total diametrical length of the section and *r* is the radius of an arc (Fig. 4). Rearranging Eq. 1 $l_a = l_d\,.\,\pi/2$.

Therefore rolling a section of *n* arcs flat increases its diametrical length by a factor of 1.57 times (see Fig. 8B).

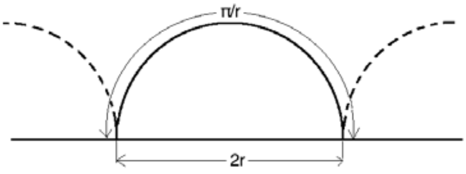

Figure 4: Portion of a section of n semicircular arcs of radius r. The arc length is π/r and the diametrical length is 2r, hence the ratio of the arc length to the diametrical length is π/2.

A/V ratio of a cuboidal segment

Consider a hypothetical cuboidal segment with square cross section and length *L*.

$$A_{cub}/V_{cub} = 4\,x\,L/4\,x^2\,L = 1/x \qquad (2)$$

where A_{cub} is the surface area (upper plus lower surfaces only) of the cuboidal segment exposed to the external environment, V_{cub} is the volume of the segment and *x* is half the length of a side of the square cross section (Fig. 5).

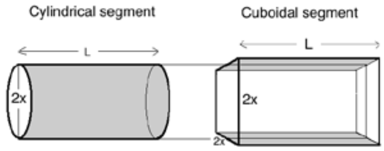

Figure 5: Cylindrical and cuboidal segments. Lateral view. Shaded area indicates surface in contact with external watery environment.

A/V ratio of a cylindrical segment

Consider a hypothetical cylindrical segment of the length *L*.

$$A_{cyl}/V_{cyl} = \pi\,2x\,L/\pi\,x^2\,L = 2/x \qquad (3)$$

where A_{cyl} is the surface area of the cylindrical segment exposed to the external environment, V_{cyl} is the volume of the cylindrical segment and *x* is the radius of the cylinder (Fig. 5).

A/V ratio of a hypothetical Dickinsonia constructed of tapering cuboidal segments

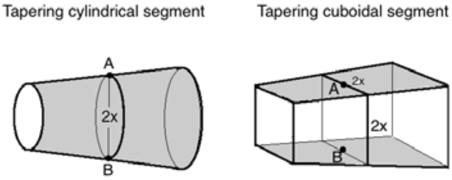

Figure 6A: Tapering cylindrical (conical frustum) and tapering cuboidal (square frustum) segments. With reference to points A and B, see Fig. 11 and 12.

$$A_{Dtcub}/V_{Dtcub} = 2\,\pi\,R^2/\pi\,R^2\,2x\ = 1/x \qquad (4)$$

where A_{Dtcub} is the surface area of a tapering cuboidal segment (square frustum), (upper plus lower surfaces only) exposed to water,

V_{Dtcub} is the volume of the segment, R = half the mean overall diameter of the *Dickinsonia* and x = half the mean thickness of the *Dickinsonia* (Fig. 6A and B).

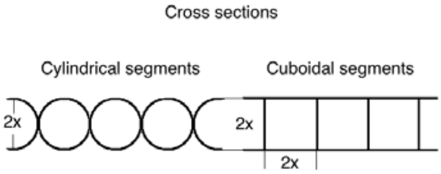

Figure 6B: Portion of the cross section of a hypothetical Dickinsonia constructed of either cylindrical or cuboidal segments.

A/V ratio of a hypothetical Dickinsonia constructed of tapering cylindrical segments

$A_{Dtcyl}/V_{Dtcyl} = (\pi R)^2/(\pi R)^2 x/2 = 2/x$ (5)

where A_{Dtcyl} is the surface area of tapering cylindrical segment (conical frustum) exposed to water and V_{Dtcyl} is the volume of the segment. R and x as in (4) (Fig. 6A and B).

Note: This hypothetical calculation assumes that there is no loss in surface area of a cylindrical segment at the junctions between segments (see Discussion).

Factors affecting the rate of diffusion of oxygen

Fick's first law

$\partial v/\partial t = A.\ D.\ \partial c/\partial x$ (Prosser, 1961) (6)

where $\partial v/\partial t$ = volume of oxygen ∂v that diffuses in time ∂t, A = the area of the surface across which the oxygen diffuses into the tissue , D = the diffusion coefficient of oxygen in the tissue, ∂x = the distance the oxygen diffuses into the tissue and ∂c = the concentration gradient of oxygen in the tissue, that is, the difference in the oxygen concentration from the beginning to the end of the diffusion distance ∂x.

The maximum diffusion distance for oxygen in a cuboidal segment of connective tissue

$$s = \sqrt{C_0 2 D_{CT} / M_{CT}}$$

(Warburg, 1923; Alexander, 1971) (7)

where s = half the thickness in millimetres (mm) of a viable cuboidal segment of connective tissue in which oxygen diffuses from both upper and lower surfaces, C_0 = the difference in oxygen concentration, expressed as a fraction of one atmosphere, from either surface of the segment to half its thickness where the oxygen concentration falls to zero, D_{CT} = the diffusion coefficient of oxygen in connective tissue in millilitres (ml) of oxygen diffusing per cubic centimetre of surface area per minute at a pressure gradient of one atmosphere per centimetre of tissue thickness (= 0.11×10^{-4}), M_{CT} = the rate of oxygen consumption of connective tissue in ml of oxygen per gram of tissue per minute (=1/600).

The maximum diffusion distance for oxygen in a cylindrical segment of connective tissue

$$r = \sqrt{C_0 4 D_{CT} / M_{CT}}$$

(Fenn, 1927; Alexander, 1971) (8)

where r = maximum radius of a viable cylinder of connective tissue in mm, C_o = the difference in the oxygen concentration, expressed as a fraction of one atmosphere, from the surface of the cylindrical segment to its central axis where the oxygen concentration falls to zero. D_{CT} and M_{CT} as in (7).

Source of data for the analysis of profile thickness to diameter in *Dickinsonia*

Retallack (2007) measured the width, length and profile depth of 94 specimens of *Dickinsonia* from the Flinders Ranges. Data from 60 of these specimens, where Retallack gave complete measurements for the specimens, have been analysed. In order to measure the profile depth or thickness of each fossil, Retallack (2007) used a device called a depth gauge with which he measured the "general levels rather than details of the ribbing". In order to take into account the inevitable variability of such measurements, Retallack's profile thickness measurement is assumed to be the average profile thickness of a specimen. The diameter was calculated for each specimen by averaging its length and width values.

Estimation of atmospheric oxygen during the Ediacaran Period

The present partial pressure of oxygen in the atmosphere at sea level, ignoring water vapour pressure, is 21.3 kilopascals (kPa). Canfield (2005) estimated the levels of atmospheric oxygen over the last billion years. Using this graphical information as the basis for calculations in the present paper, the atmospheric partial pressure of oxygen during the Ediacaran period was estimated to be 4, 8 and 12 kPa at the beginning, middle and end of the Ediacaran period respectively.

Oxygen consumption of Ediacaran connective tissue

The specific nature of the tissue components of Ediacaran organisms is unknown. However one histological component that would *a priori* be expected to compose a portion of the organism is connective tissue. Connective tissue consists largely of fibroblasts and a non-cellular component called extracellular matrix (ECM), which is secreted by the fibroblasts. ECM forms the framework of metazoan organisms and binds their cells together. Collagen is the major component of ECM (Cell Biology @ Yale, 2014). Genetic studies indicate that collagen has remained remarkably constant throughout the evolution of animals (Garrone, 1999). It therefore seems likely that fibroblastic cells, not unlike those of today, produced collagenous ECM in the Ediacarans. Furthermore it would be most unlikely that Ediacaran connective tissue would have a rate of oxygen consumption greater than it is today; if anything it would be expected to be less (Mills, 2014). Therefore the conservative assumption will be made here that the rate of oxygen consumption in connective tissue during the latter part of the Ediacaran period was the same as it is today.

Graphical representation of the oxygen concentration gradient

The theoretical concentration gradient of oxygen from ocean water into the tissue of segmental Ediacarans under consideration can be represented graphically (Fig. 7) (Alexander, 1971; Math Bench, 2014). The concentration of oxygen in well-mixed ocean water is assumed to be directly proportional to the partial pressure of oxygen in the atmosphere in contact with the water (Henry's law), consequently the Ediacaran tissue oxygen concentration gradient can also be represented as a gradient of oxygen partial pressure (Krogh, 1941). The precise three dimensional pattern of oxygen diffusion through living tissue is highly complex, never-the-less this representation of the oxygen concentration gradient provides a workable basis for the purpose of a comparison of cylindrical and cuboidal forms in the present study.

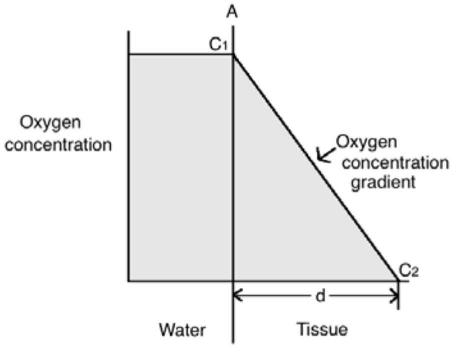

Figure 7: Graphical representation of the oxygen concentration in the water of the external environment and in the tissue of the internal environment of an organism. The two environments come into contact at A. Oxygen concentration is shown on the vertical axis and distance on the horizontal axis. C_1 is the concentration of oxygen in the water bathing the organism. d is the maximum distance that oxygen diffuses in time t at which point the oxygen concentration has decreased to C_2. The straight line joining C_1 and C_2 represents the theoretical oxygen concentration gradient.

Results and Discussion

Segmental structures in *Pteridinium* and *Dickinsonia*

The fossils of many species of Ediacaran appear to be sheet- or sail-like, that is they are relatively thin in cross section compared with their overall size. An example of this form of Ediacaran is *Pteridinium* (Fig. 2) that appears to have consisted of three elongated leaf-like structures called vanes (Richter, 1955; Seilacher, 1989). The surfaces of these vanes are divided transversely into multiple parallel segments (Narbonne, 1997). Underlying this surface segmentation, Seilacher (1989) envisaged compartments which he called the "quilted pneu structure". He believed that this structure could be applied to a range of Ediacarans, including *Pteridinium* and *Dickinsonia* (Fig. 1). Grazhdankin (2002) suggested these box-like chambers ended blindly at both ends, were supported hydrostatically by enclosed sediment and could be represented schematically as cuboids of square cross section.

Jenkins' (1992) drawing of the cross section of a *Pteridinium* vane from a fossil specimen was suggestive that at least some chambers of the vane were actually more circular than square in cross section and approximately 1.6 mm in diameter. Recent photographic evidence (Elliott, 2011) further supports the concept that a *Pteridinium* vane may have been composed of a single row of tubules of approximately 1.6 mm diameter. Grazhdankin (2002) suggested that a segment could collapse with partial to complete flattening. Such flattening would be expected to result in an increase in the width of the surface segmentation with a proportionate decrease in the segment depth. For example complete collapse of a cylindrical segment with an initial circular diameter of 1.6 mm would theoretically result in a flattened segment width of 2.5 mm, that is, similar to widths of segments measured by Richter (1955) in the first detailed study of *Pteridinium.*

In general the segments in *Pteridinium* do not taper greatly from one end to the other. In the oval shaped *Dickinsonia* on the other hand, the segments fan out from a mid-line ridge and their width generally increases from the midline to the periphery (Fig. 1 and 3). The larger the *Dickinsonia* the greater the number of segments and the profile of the corrugations becomes flatter (Sprigg, 1949; Seilacher, 1989). Consequently the mean width of a *Dickinsonia* segment tends to remain remarkably constant regardless of the overall size of different specimens.

Effect of corrugations on surface area

The surface segmentation is corrugated to a varying extent in the fossils of both *Pteridinium* and *Dickinsonia*. An important question is "What was the shape of the cross section in the living segments?" since the cross sectional shape of the segment influences the surface area for oxygen diffusion (Eq. 6). One could consider a range of possibilities by progressively morphing the segment from a purely cuboidal to a purely cylindrical form.

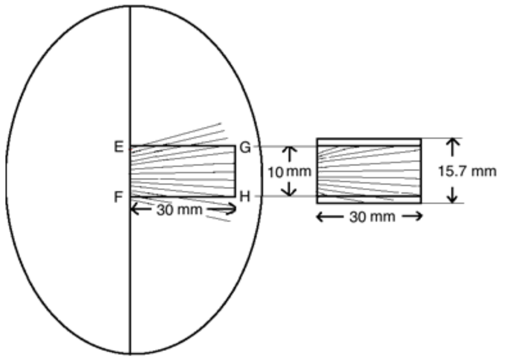

Figure 8A: Effect of segmentation on the theoretical surface area in Dickinsonia (Fig. 1 shows the original specimen). Consider a rectangular area EFGH on the fossil's surface of width 10 mm and radial length 30 mm from the midline. This 10 mm width is found to enclose 12 segments adjacent to the midline, section EF, and half this number at the radial distance of 30 mm from the midline, section GH. Assuming that the cross section of each segment is a perfect semicircle, then if this rectangular corrugated area is rolled flat, the resulting flat area would be increased by $\pi/2$ or 1.57 times (Eq. 1) (Note: diagram is not strictly to scale).

In a surface composed of segments of perfectly semicircular cross section, the surface area is increased by a factor of $\pi/2$, that is 1.57 times, compared with a surface made up of perfectly flat surfaced segments (Eq. (1); Fig. 4). Thus within any rectangular area of the surface of any given width and radial length, the increase in the surface area due to the contained corrugations is independent of the number of segments. A larger number of segments of smaller radius has the same rolled flat length as a smaller number of segments of larger radius (Fig. 8A and 8B).

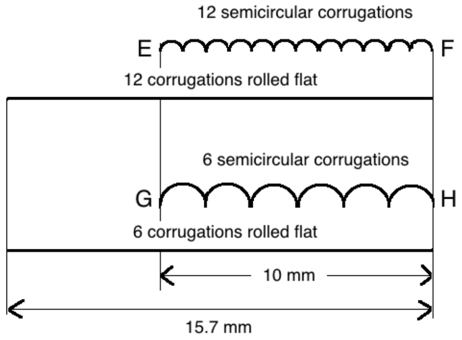

Figure 8B: If the semicircular segments in sections EF and GH, as shown in Fig. 8A, are rolled flat, they will both measure the same length despite the fact that EF contains 12 semicircular segments and GH six segments.

Thickness versus diameter in *Dickinsonia*

The majority of the 60 fossils specimens had a profile thickness of less than 2.5 mm and the mean thickness was 1.42 ± 0.96 mm (± standard deviation) (Fig. 9). The mean value of all of the diameters of these specimens was 52.7 ± 41.0 mm. The greatest diameter of an individual fossil was 259 mm. Clearly *Dickinsonia* is generally very thin in relation to its diameter.

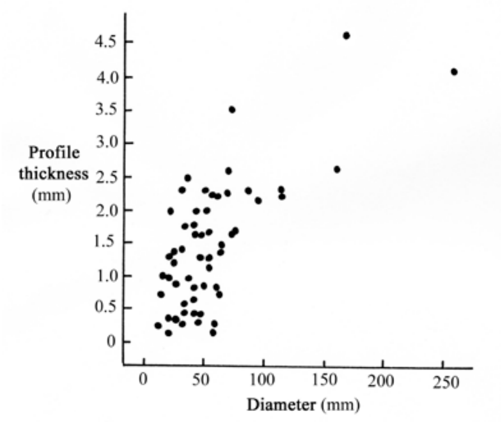

Figure 9: Profile thickness (mm) versus diameter (mm) in Dickinsonia fossils (n=60; based on raw data from Retallack, 2007).

Argument for a three dimensional tapering structure of *Dickinsonia* segments

As already discussed the surface appearance of the segmental corrugations of *Dickinsonia* clearly shows that the segments taper from periphery to midline. Seilacher (1989) showed that segmentation exists on both the upper and lower surfaces of *Dickinsonia.* The following analysis is based on the hypothesis that *Dickinsonia* consisted of a single layer of segments and that these structures tapered from the periphery to the midline. Each segment will be considered as either a tapering cuboid (square frustum) or tapering cylinder (conical frustum) (Fig. 6A).

A/V ratio in *Dickinsonia* composed of tapering cuboidal or tapering cylindrical segments

The A/V ratio of 60 fossil specimens of *Dickinsonia* was calculated on the theoretical basis that the structure consisted of either tapering cylindrical or tapering cuboidal segments (Eq. (4) and (5)). *Dickinsonia* with the smallest overall fossil diameters had the highest A/V ratios. The graph of the individual data points indicates that at an average diameter of approximately 50 mm the steep decline in the A/V ratio approaches a lower limit and does not decrease significantly below this ratio despite a considerable increase in the diameter of the organism (Figs. 10A and 10B).

In the case of a hypothetical *Dickinsonia* composed of tapering cylindrical segments this lower limit of the A/V ratio is approximately two and in the case of a *Dickinsonia* based on tapering cuboidal segments it is approximately unity (Fig. 10A and B).

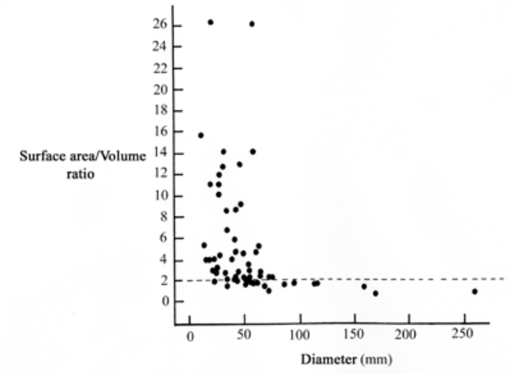

Figure 10A: Surface area to volume (A/V) ratio versus diameter (mm) in Dickinsonia fossils of known profile thickness and diameter but assuming that they are composed of tapering cylindrical segments (n=60; based on raw data from Retallack, 2007). Dotted line indicates an A/V ratio of 2.0.

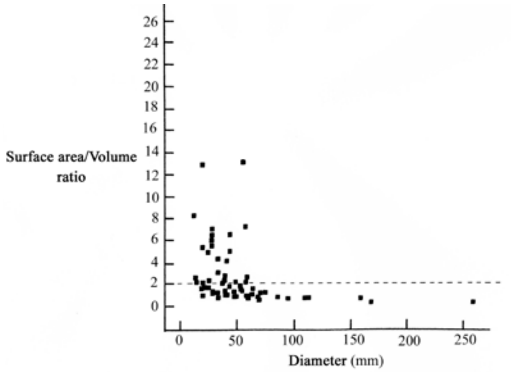

Figure 10B: Surface area to volume (A/V) ratio versus diameter (mm) in the same Dickinsonia fossils as shown in Fig. 9A but assuming that they are composed of tapering cuboidal segments. Dotted line indicates an A/V ratio of 2.0.

In the analysis of the hypothetical structure of *Dickinsonia* based on tapering cylindrical segments, there is theoretically no loss in surface area at the point of contact between adjacent cylinders. On the other hand in the case of the tapering cuboids, half the surface area is lost as a result of the contact between adjacent segments. The theoretical A/V ratio in the cylindrical segment was $2/x$ and in the cuboidal segment $1/x$ (Eq. (2) and (3)). Since x, half the mean thickness of a segment, is the same in both cases, it is clear that the A/V ratio of the cylindrical structure is twice that of the cuboidal structure. It is also clear that progressively morphing from a purely cylindrical form to a purely cuboidal form will progressively reduce the difference in A/V ratio from two to one as the area of contact between adjacent segments increases. The actual structural form of the segments in Ediacarans like *Pteridinium* and *Dickinsonia* would be expected to be the result of competitive evolutionary pressure which on one hand would tend to maximise the A/V ratio and on the other maximise the structural strength of the connection between adjacent segments.

Oxygen concentration gradient in a cuboidal segment and a cylindrical segment

At the time of the first non-mobile forms of Ediacarans, approximately 580 million years ago, the partial pressure of the oxygen in the atmosphere is estimated to have been 9.3 kPa and at the time of the first mobile Ediacarans 555 MYA 12 kPa (Fike, 2006). *Pteridinium* and *Dickinsonia* are believed to have co-existed during the latter part of the Ediacaran period. Therefore the estimate of 12 kPa will be used in the present analysis. The segments are assumed to be biological structures filled with living connective tissue (see Methods).

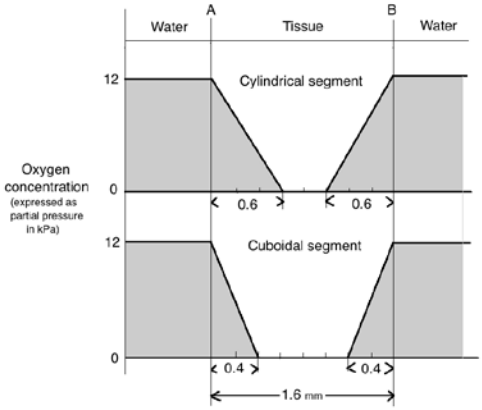

Figure 11: Theoretical oxygen concentration gradient from ocean water into a cylindrical and cuboidal segment with ultra-thin segmental walls at A and B that have no effect on oxygen diffusion. With reference to points A and B see Fig. 6A.

In the initial analysis the wall separating the seawater from the living tissue of the segment is assumed to be a thin membrane with no significant effect on oxygen diffusion (Fig. 11). The oxygen concentration profile along a straight line between points A and B is examined (see also Fig. 6A). The distance between these points, that is the thickness of the segment, is taken to be 1.6 mm (see earlier).

In the case of a cuboidal segment, the maximum oxygen diffusion distance was 0.4 mm (Eq. (7)). Thus oxygen diffusing from points A and B would fail to reach the centre of the cuboidal segment leaving an anoxic gap of 0.8 mm in the central region of the segment. On this basis the cuboidal segment would not have been viable.

In the case of the cylindrical segment, the maximum diffusion distance is 0.6 mm (Eq. (8)). In this case however the anoxic gap is halved to 0.4 mm, but the cylindrical segment would still not be viable.

Effect of a segmental wall on the oxygen concentration gradient

Dzik (1999) suggested that the apparently flexible walls of the segments of Ediacarans were probably composed of "collagenous fabric". He argued that these collagenous sheaths were more resistant to post-mortem decay than the presumed cellular contents of the segments and therefore more likely to be fossilised. He proposed that the segmental walls were relatively thick. Recent three-dimensional microCT findings of Meyer (2014) indicate that the walls of *Pteridinium* were flexible and therefore consistent with a composition of connective tissue. They also reported that their findings support the "traditional interpretation" of a semi-benthic or epibenthic lifestyle.

The diffusion coefficient of oxygen in acellular collagenous gel is approximately 2.5 times greater than that in connective tissue (Krogh, 1919). It is generally held that the former material, as in mesogloea, is "metabolically inert", that is it consumes virtually no oxygen (Chapman, 1953; Bouillon, 1968; Raff, 1970). The combined effect of these two factors, a greater oxygen diffusion coefficient and a negligible oxygen consumption, would be expected to result in a considerable increase in the rate of diffusion of oxygen through a collagenous wall compared with the same thickness of living connective tissue (Eq. (7) and (8)). A comparative study by Schick (1979) on sea anemones supports this basic concept.

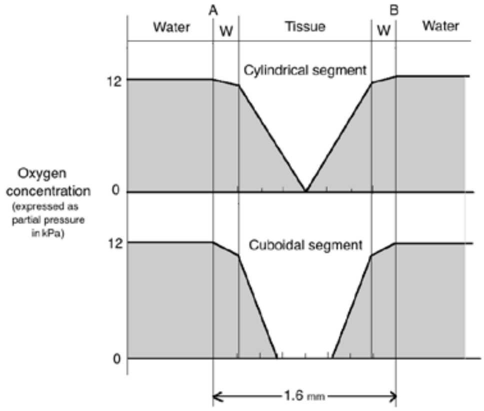

Figure 12: Theoretical oxygen concentration gradient from ocean water into a cylindrical segment and cuboidal segment with 0.2 mm thick collagenous segmental walls, W, at A and B. With reference to points A and B see Fig. 6A.

If it is assumed conservatively that the metabolic rate of an acellular collagenous wall is 1/10th that of living connective tissue and its oxygen diffusion coefficient is 2.5 times greater than connective tissue (see earlier), then the maximum diffusion distance for oxygen in a cylinder of collagenous gel would be 3.0 mm (substitution in Eq. (8)), which is a five fold increase in the maximum diffusion distance compared with that in living connective tissue. Thus a collagenous segmental wall would be expected to significantly increase the maximum depth of oxygen diffusion into the segment (Fig. 12). Assuming a wall substance with such characteristics, it is found that in order for oxygen to reach the centre of a 1.6 mm thick cylindrical segment containing living connective tissue, the wall thickness of the segment would need to be approximately 0.2 mm. On the other hand, if a cuboidal segment of connective tissue had the same wall thickness, there would remain a central anoxic gap of 0.5 mm and this structure would still be not be viable (Fig. 12).

Recently Laflamme (2009) modelled *Pteridinium* on the basis of a cuboidal structure and analysed the A/V ratios for a range of sizes. These workers assumed that their cuboidal structure was hollow and examined wall thicknesses from 1.6 mm to 0.01 mm. They found that such structures with a A/V ratio of around one had a wall thickness of 1.6 – 0.5 mm. Similarly the present study determined that a *Pteridinium* vane constructed of cuboidal segments made of solid tissue 1.6 mm thick, an A/V ratio of 1.25 (substituting in Eq. (2), 1/0.8) would be inadequate to supply oxygen the 0.8 mm distance to the centre of the structure (see Fig. 11 and 12). They came to the conclusion that for their hollow cuboidal structure to be viable it would require oxygen diffusion from both the inner and outer surfaces with a thin component of living tissue of less than 0.5 mm thickness and with the segments open at one end to allow the entry of ocean water. However with only a single opening, stagnation of water with hypoxia would be expected in such a chamber with little improvement in oxygen supply. Also segmental openings along the free edges of the vanes in *Pteridinium* fossils have not been observed to date.

Laflamme (2009) did not examine a cylindrical form of segmentation nor did they specifically analyse their cuboidal structure in relation to oxygen diffusion. Interestingly, however, they determined that megabacteria which rely upon diffusion for their oxygen supply generally have A/V ratios of approximately two or greater. The present study of *Dickinsonia* found that the majority of specimens analysed also had an A/V ratio of two or greater when this ratio was calculated on the basis of a cylindrically segmented structure.

Habitus and the oxygen concentration gradient in *Dickinsonia*

It has been suggested that *Dickinsonia* was a mobile Ediacaran and able to seek out its food supply (Seilacher, 1989; Gehling, 2005). If it is assumed that *Dickinsonia* was constructed of tapering cylindrical segments of maximum thickness of approximately 1.6 mm, this study has shown that such a segmented structure could have provided adequate oxygenation provided that oxygen was free to diffuse into the tissue from both sides of the segment. However at times *Dickinsonia* may have remained stationary in order to digest the underlying biomat (Fig. 3).

Under these conditions the ocean water trapped beneath the organism could have become increasingly stagnant and hypoxic. A significant reduction in oxygen partial pressure would have been unlikely in the segmental tissue near the periphery of the organism since the surface corrugations would have facilitated access to fresh ocean water (Fig. 3, diffusion path LM). More at risk might have been the segmental tissue closer to the midline of the organism (Fig. 3, diffusion path NP). However if the segments tapered in thickness towards the midline, as suggested in this study, then the tissue diffusion distance would be progressively reduced towards the centre of the *Dickinsonia* thereby facilitating an adequate oxygen supply from the upper surface alone if necessary.

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