

# Rangeomorphs, *Thectardis* (Porifera?) and dissolved organic carbon in the Ediacaran oceans

E. A. SPERLING,<sup>1,2</sup> K. J. PETERSON<sup>3</sup> AND M. LAFLAMME<sup>1</sup>

<sup>1</sup>Department of Geology and Geophysics, Yale University, New Haven, CT, USA

<sup>2</sup>Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA, USA

<sup>3</sup>Department of Biological Sciences, Dartmouth College, Hanover, NH, USA

## ABSTRACT

The mid-Ediacaran Mistaken Point biota of Newfoundland represents the first morphologically complex organisms in the fossil record. At the classic Mistaken Point localities the biota is dominated by the enigmatic group of “fractally” branching organisms called rangeomorphs. One of the few exceptions to the rangeomorph body plan is the fossil *Thectardis avalonensis*, which has been reconstructed as an upright, open cone with its apex in the sediment. No biological affinity has been suggested for this fossil, but here we show that its body plan is consistent with the hydrodynamics of the sponge water-canal system. Further, given the habitat of *Thectardis* beneath the photic zone, and the apparent absence of an archenteron, movement, or a fractally designed body plan, we suggest that it is a sponge. The recognition of sponges in the Mistaken Point biota provides some of the earliest body fossil evidence for this group, which must have ranged through the Ediacaran based on biomarkers, molecular clocks, and their position on the metazoan tree of life, in spite of their sparse macroscopic fossil record. Should our interpretation be correct, it would imply that the paleoecology of the Mistaken Point biota was dominated by sponges and rangeomorphs, organisms that are either known or hypothesized to feed in large part on dissolved organic carbon (DOC). The biology of these two clades gives insight into the structure of the Ediacaran ocean, and indicates that a non-uniformitarian mechanism delivered labile DOC to the Mistaken Point seafloor.

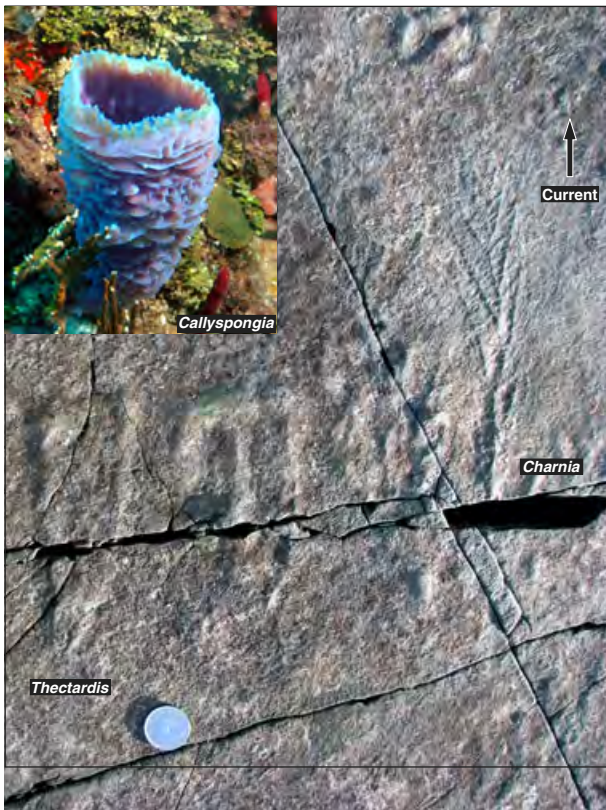
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Corresponding author: Dr. E. A. Sperling. Tel.: 203-927-3754; fax: 617-495-8839; e-mail: Sperling@fas.harvard.edu

## INTRODUCTION

The mid-Ediacaran Mistaken Point biota, located on the Avalon Peninsula of Newfoundland, Canada, represents the oldest large and morphologically complex organisms in the fossil record (Narbonne, 2005; Xiao & Laflamme, 2009). Fossils first appear in the Drook Formation, closely following the Gaskiers glaciation (Narbonne & Gehling, 2003), and soon after evidence for an increase in the amount of dissolved oxygen in the water (Canfield *et al.*, 2007). The fossils are preserved beneath ash beds (“Conception-style” preservation of Narbonne, 2005), providing a near-census view of an Ediacaran seafloor. Sedimentological and stratigraphic studies have demonstrated that the organisms were living in a deep-water turbidite system (Wood *et al.*, 2003; Ichaso *et al.*, 2007), well below the photic zone, thereby ruling out the possibility that they relied on photosynthesis. By far the most common fossils at Mistaken Point localities are rangeomorphs (Brasier & Antcliffe, 2009; Narbonne *et al.*, 2009), which

comprise upwards of 75% of all taxa at Mistaken Point and ~99% of organisms on the so-called D and E surfaces in the Mistaken Point Ecological Reserve (Clapham *et al.*, 2003). Exquisitely preserved fossils from Spaniards Bay suggest that rangeomorphs were constructed of iterated cm-scale architectural elements that show self-similarity (“fractal” architecture) over at least four scales (Narbonne, 2004; Narbonne *et al.*, 2009). Although rangeomorphs dominate the classic Mistaken Point localities, another taxon, *Thectardis avalonensis*, is the most common fossil on the Pigeon Cove surface in the Drook Formation, ~1500 meters lower stratigraphically (Clapham *et al.*, 2003, 2004). Like many fossils in the Mistaken Point biota, *Thectardis* was referred to by a colloquial name, “triangle,” for many years in the literature until formally named by Clapham *et al.* (2004). It is conspicuous as one of the few organisms in the biota that does not have a “fractal” construction. *Thectardis* fossils have higher relief along the sides and the rim and are current aligned in the same direction as other benthic epifaunal fronds such as *Charnia*



**Fig. 1** The Ediacaran fossil *Thectardis avalonensis* from the mid-Ediacaran (<580 Ma) of the Avalon Peninsula, Newfoundland, Canada. Diameter of Canadian quarter = 23.81 mm. *Thectardis* fossils are consistently oriented parallel to fronds, such as the *Charnia antecedens* holotype, indicating that they were originally erect and felled by currents. From the upper Drook Fm. at Pigeon Cove, Newfoundland. (Inset) Modern vase sponges show a form similar to the reconstruction of *Thectardis* by Clapham *et al.* (2004) and demonstrate that the fossil is consistent with the hydrodynamics of the sponge body plan. Image kindly provided by Robert Aston.

*antecedens* (Fig. 1), indicating that the original life position of *Thectardis* was erect. This evidence allowed Clapham *et al.* (2004) to reconstruct *Thectardis* as a cone with the apex sticking into a microbial mat at the sediment–water interface. After felling, the preservation of this structure results in the “triangle” outline. Interestingly, the reconstructed morphology of *Thectardis* is similar to modern vase sponges (e.g., Fig. 1 Inset), and it is clear how the felling of such a geometry would create a triangular-shaped fossil with a raised outer rim.

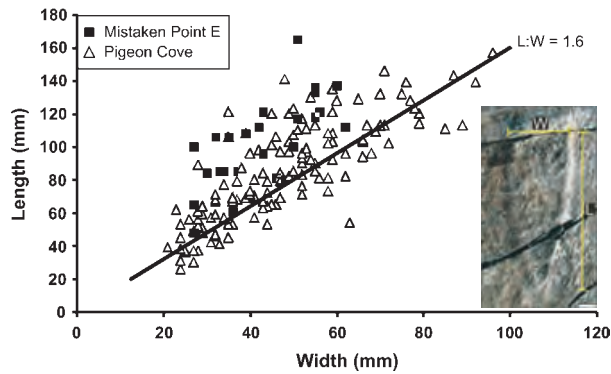
### BIOLOGICAL AFFINITY OF *THECTARDIS*

Clapham *et al.* (2004) did not interpret the phylogenetic affinity of *Thectardis avalonensis*, but its body plan, in conjunction with the inferred deep-ocean paleoenvironment, indicates that it is most likely a sponge. Sponges feed by taking water in through a series of small pores (ostia) in the external epithelium (pinacoderm). The feeding current is created by

the beating of specialized flagellated cells, the choanocytes, which are clustered in chambers along the internal epithelium (choanoderm). The combined cross-sectional area of the choanocyte chambers is larger than that of the combined incurrent canals, causing the flow to slow while passing through the chambers (Reiswig, 1975), where bacteria and dissolved organic carbon (DOC) are removed by the choanocytes through phagocytosis and pinocytosis. The water then exits through an osculum or oscula, which has a cross-sectional area smaller than the combined incurrent pores, causing the exhaled water to be forced away from the sponge, thus avoiding recycling. Importantly, studies of the aquiferous systems of three marine demosponges demonstrated that the hydraulic parameters of their water-canal systems are similar despite divergent external morphologies, and in all three cases the cross-sectional area of incurrent ostia comprised between 22% and 30% of the inhalant surface (Reiswig, 1975). Hence, sponge physiology is independent of gross morphology, but instead is based on hydrodynamic principles (Brusca & Brusca, 2003).

These hydrodynamic relationships then allow a simple test to determine whether a fossil organism could have been a sponge (Sperling *et al.*, 2007). A perfectly conical sponge will require a length–width ratio greater than  $\sim 1.6$  to ensure that the inhalant surface area is equal to or greater than that of the osculum. This number represents a conservative estimate, as it assumes the fossils have not experienced any lateral expansion during decay or compaction. Such lateral expansion is expected to be rare in fossils such as *Thectardis* (e.g., Briggs & Williams, 1981), but if it did occur, the full flattening of a cone to a 2D plane would reduce the necessary length–width ratio to  $\sim 1.1$ . The functional expectation for a viable water-canal system is met by the morphometric data collected for *Thectardis* by Clapham *et al.* (2004), who found length-to-width ratios ranging from  $\sim 1.4$  to 4 (Fig. 2). Some specimens plot below the minimum 1.6 length–width ratio, but the vast majority, including all specimens from the Mistaken Point E surface, exceed it comfortably. Where fossils approach the minimum length–width ratio this may reflect: (i) minor crenulations in the body, which are not preserved but would have served to increase the inhalant surface area, (ii) departures from a conical shape to a more tubular upper part, which increases the inhalant surface area relative to oscular area with respect to a true cone, and (iii) imperfect restoration of the original proportions – retrodeformation of the Mistaken Point fossils is not precise. All specimens below the 1.6 ratio are from the Pigeon Cove surface in the Drook Formation, where in contrast to the E surface at Mistaken Point, the lack of circular frond holdfasts makes retrodeformation particularly difficult.

As reconstructed, *Thectardis* meets the requirements for a functional water-canal system, with water drawn in through the walls of the “triangle” and exhaled via the osculum. Nonetheless, *Thectardis* does not show physical evidence of



**Fig. 2** Length–width data for the Ediacaran fossil *Thectardis* from Clapham *et al.* (2004). Sponges usually have an oscula (or combined excurrent pores) with an area less than the area of the combined incurrent pores. This expels the excurrent water away from the sponge to avoid recycling. For a perfectly conical sponge, the length (height) should be  $\sim 1.6$  times the width (diameter of oscula) in order to maintain an oscular area greater than the area of the combined incurrent pores. This ratio assumes the fossils preserve their original dimensions (Briggs & Williams, 1981); flattening of the fossils would result in an artificially inflated width, and the required ratio would consequently range between 1.1 and 1.6 depending on the degree of flattening. This hydrodynamic principle is met by the majority of specimens of *Thectardis* measured by Clapham *et al.* (2004). Some points do fall slightly below the 1.6 ratio, but this can be explained by (i) flattening during fossilization resulting in a longer apparent width, (ii) minor crenulations in the body wall that increase inhalant surface area, (iii) departure from a perfect cone to a more tubular shape, and (iv) errors in the retrodeformation process necessary to remove the effects of tectonics. All specimens falling below the 1.6 minimum ratio are from the Pigeon Cove surface in the Drook Formation, where the lack of circular frond holdfasts makes retrodeformation especially difficult.

the ostia, although this is not unexpected given these are on the order of 5–50  $\mu\text{m}$  (Reiswig, 1975; Mackie & Singla, 1983), and are to our knowledge not preserved in any fossil sponge. Despite this absence, acquiring nutrients via a water-canal system is about the only viable means of feeding for *Thectardis* – as the Mistaken Point sediments were deposited beneath the photic zone (Wood *et al.*, 2003), algal affinities are ruled out, as is a eumetazoan affinity given the absence of a clear archenteron, mouth or food-capturing structure, and movement. A fungal affinity is also unlikely given that there is no evidence of saprophytism and no obvious way the organism could feed within the context of the sediment/bacterial mat. And the absence of a fractal architecture suggests that *Thectardis* is not feeding passively on dissolved nutrients in the water column like the rangeomorphs (Sperling *et al.*, 2007; Laflamme *et al.*, 2009). In summary, although the arguments for a sponge affinity are primarily functional, other possibilities are difficult to reconcile with requirements for nutrition.

The recognition of a sponge body plan for *Thectardis* does not constrain its phylogenetic position precisely. The phylogenetic relationships of extant sponges are contentious; recent molecular phylogenetic studies consistently resolve them as sister to all other animals, but whether they are monophyletic or paraphyletic is under debate (Philippe *et al.*, 2009; Sperling

*et al.*, 2009). *Thectardis* does not show any characters that align it with a modern sponge group, but this may simply reflect the nature of its preservation. For instance, no spicules are evident, which could either be a preservational issue, as sponge spicules are dissolved in many settings, both modern (Land, 1976; Rutzler and Macintyre, 1978) and ancient (Narbonne & Dixon, 1984; Mock & Palmer, 1991), or reflect a real biological absence. But as spicules are unlikely to be primitive for sponges and probably evolved convergently in several different lineages (Reitner & Mehl, 1996; Sperling *et al.*, 2007), their absence does not negate a sponge affinity. The lack of spicules, if real, does suggest that *Thectardis* is not a member of a crown-group characterized by spicules (Calcarea, Hexactinellida, Democlavia + Haplosclerida; Sperling *et al.*, 2009). If “sponges” are paraphyletic with multiple independent origins of spicules, it is likely that there was a series of extinct lineages, with or without spicules, along the metazoan and eumetazoan stem-lineage. In this case an osculum is a plesiomorphy of a paraphyletic sponge grade, allowing *Thectardis* to be identified as a probable total-group metazoan, representing an extinct lineage anywhere below Eumetazoa (or even as a stem-placozoan if the placozoan feeding sole is not homologous to the eumetazoan endoderm; Sperling & Vinther, 2010), but without further phylogenetic precision.

The identification of *Thectardis* as a likely sponge helps address a conundrum in both the Mistaken Point biota and Ediacaran paleontology in general. Both molecular clocks (Sperling *et al.*, 2010) and the organic geochemical record (Love *et al.*, 2009) suggest that not just sponges, but relatively derived groups of sponges, were present in the Cryogenian. Furthermore, the biomarker record demonstrates that demosponges not only were present throughout the Ediacaran, but were abundant enough, at least locally, to make quantitative contributions to the sediment sterol record (Love *et al.*, 2009). Thus, the paucity of Ediacaran sponge fossils is anomalous. *Palaeophragmodictya* from the classic Ediacara deposits in South Australia likely represents a sponge (Gehling & Rigby, 1996), and *Rugoconites*, *Albumares* and *Tribrachidium* (the so-called “sand sponges”) from the same deposits have also been interpreted as sponges (Seilacher *et al.*, 2003). Spicules and sponge body fossils have been reported from the Doushantuo Formation in South China (Li *et al.*, 1998), but these features may represent diagenetic artifacts (Yin *et al.*, 2001). In the Cryogenian, sedimentary fabrics comparable to those generated by sponges, or more broadly the decay of collagenous organisms, are present in the >779 Ma Little Dal Formation in northwestern Canada (Neuweiler *et al.*, 2009), and globular fossils with internal canals are present in the Trezona Formation of South Australia (Maloof *et al.*, 2010). The aforementioned fossils convince as sponges to varying degrees, but with the exception of the Trezona forms, none are especially common, and they are still relatively widely spaced temporally. The recognition that *Thectardis* likely



represents a sponge, and one that is locally abundant in some horizons, provides additional body fossil evidence for this phylum in the Ediacaran. Furthermore, the recognition of sponges in the Mistaken Point biota provides evidence for the presence of two independently derived strategies for feeding on DOC (Sperling *et al.*, 2007), suggesting strong selection pressures for the exploitation of this food resource in the Precambrian ocean and giving insight into the dynamics of DOC in the Ediacaran deep ocean.

## DOC FEEDING IN THE MISTAKEN POINT BIOTA

The idea that Ediacaran organisms may have gained their nutrition through osmotrophy was advanced by Seilacher (1984, 1985), and McMenamin (1993, 1998), who suggested that it could be the most important Ediacaran feeding mechanism. Key to the arguments by McMenamin was the then-novel data from Sugimura & Suzuki (1988) that modern surface ocean water contains at least twice as much DOC as previously realized. Ironically, these values for the modern ocean were eventually found to be inaccurate (see Hedges, 2002 for historical perspective), but actually far less than some current hypotheses for DOC levels in the Neoproterozoic ocean (Rothman *et al.*, 2003). More specific claims for DOC feeding by Ediacaran organisms were not possible until the discovery of exceptionally preserved rangeomorph fossils at Spaniards Bay, Newfoundland (Narbonne, 2004). These fossils show no evidence of openings, even at the finest scale (1/10th of a mm). Combined with a paleoenvironment below the photic zone and a “fractal” architecture which would maximize the surface-area-to-volume ratio, this prompted Sperling *et al.* (2007) and Laflamme & Narbonne (2008) to hypothesize that rangeomorphs fed by direct absorption of dissolved organic matter. Modeling of rangeomorph growth demonstrated that these organisms could have achieved surface-area-to-volume ratios similar to modern osmotrophic bacteria (Laflamme *et al.*, 2009). The comparison with osmotrophic bacteria makes these calculations extremely conservative, as invertebrate larvae can meet most or all of their energy budgets from DOC (Jaecle & Manahan, 1989a,b; Shilling & Manahan, 1990), and heterotrophic protists such as choanoflagellates can subsist in axenic cultures solely on DOC (Gold *et al.*, 1970). Because both these forms have surface-area-to-volume ratios orders of magnitude larger than bacteria, it is clear that rangeomorphs could have functioned as osmotrophic organisms. Other potential feeding strategies for rangeomorphs, such as chemosynthesis, are unlikely. While it cannot be ruled out completely (reviewed by Laflamme *et al.*, 2007; Laflamme & Narbonne, 2008), there is no evidence consistent with chemosynthesis in either the pattern of fossil distribution or the sedimentology, such as is seen in known Phanerozoic chemosynthetic settings (Little *et al.*, 1998). In other words, although the possibility remains open that

rangeomorphs were not feeding on DOC, there is no obvious feeding strategy other than osmotrophy for a benthic, sessile organism with no apparent body openings that lived beneath the photic zone.

The recognition of *Thectardis* as a likely sponge augments the evidence for the dominance of osmotrophic DOC feeding in the Mistaken Point biota. Sponges have a mixotrophic diet, feeding opportunistically on particles small enough to pass through the ostia and be taken in by the choanocytes through phagocytosis and pinocytosis, including DOC (alternatively referred to as DOM, dissolved organic matter, in many biological and oceanography studies) at modern concentrations and a diverse mix of bacteria, archaea and microeukaryotes (Reiswig, 1971; Pile *et al.*, 1997; Ribes *et al.*, 1999; Duckworth & Pomponi, 2005; Pile & Young, 2006; Thurber, 2007). Many living sponges meet the majority of their nutritional needs from DOC (Reiswig, 1974; Yahel *et al.*, 2003; de Goeij *et al.*, 2008a,b), although the extent varies depending on species (see for example Yahel *et al.*, 2007), and some of the DOC processing is likely mediated by bacterial symbionts. Sponges are not “fractal” in the sense of rangeomorphs, but the countless microvilli of the choanocytes result in a similar high surface area. Reiswig (1975) calculated that the intervillar surface area in sponge choanocyte chambers was 12–56 times greater than the external surface area, which combined with the extraordinarily high pumping rates, results in high removal of DOC from ambient water. Yahel *et al.* (2003) found that the sponge *Theonella* gained over an order of magnitude more carbon from DOC than from living cells. As de Goeij *et al.* (2008a) noted, “these species, in spite of being classified as particle feeders, are (in quantitative terms related to the availability of organic carbon sources) actually ‘DOM-feeders’”.

The Mistaken Point biota appears to represent a deep ocean dominated by organisms that obtained much if not all of their organic carbon through osmotrophy on the DOC pool. This paleoecology indicates that Ediacaran DOC dynamics were very different from those of the modern ocean: specifically a larger quantity of labile DOC reached the deep ocean.

## DOC – A PRIMER

Dissolved organic carbon, operationally defined as organic matter that passes through a 0.2 µm filter, is one of the largest exchangeable carbon pools on the modern earth and comprises ~97% of organic carbon in the ocean (Hansell *et al.*, 2009). Because it is defined operationally, rather than genetically, DOC is a heterogeneous mix of free amino acids, sugars, humic substances, fatty acids and diagenetically altered refractory organic matter, all with different compositions, isotopic values and labilities. The majority exists in uncharacterized states – only 4–11% of DOC in surface oceans and 1–3% of DOC in deep waters have been characterized as recognizable biochemicals (Benner, 2002). In the modern, most DOC

production occurs in surface waters through a diverse range of processes including extracellular release by phytoplankton, grazing by zooplankton (including sloppy feeding, egestion and excretion), viral and bacterial lysis of cells, enzymatic hydrolysis of sinking phytoplankton, and excretion of extrapolymeric substances by bacteria (reviewed by Nagata, 2000; Carlson, 2002). Much of this new DOC, primarily free amino acids and sugars, is rapidly consumed on a timescale of minutes to days (Furhman & Ferguson, 1986; Kirchman *et al.*, 1991; Amon & Benner, 1994). The production of most new DOC in the surface ocean and its rapid consumption leads to a gradient in the modern ocean, with concentrations of  $\sim 60\text{--}90\ \mu\text{M}$  at the surface and  $35\text{--}45\ \mu\text{M}$  at depth (Hansell *et al.*, 2009). This deep dissolved carbon pool is carbon-rich compared to the surface pool (i.e., depleted in nitrogen and phosphorous), and the surface pool is itself carbon-rich compared to the C:N:P stoichiometry of primary productivity (Redfield ratio; Benner, 2002). The deep-ocean DOC is very resistant to microbial utilization (Barber, 1968) and radiocarbon ages for deepwater DOC are on the order of 4000–6000 years (Williams & Druffel, 1987; Bauer *et al.*, 1992), much slower than the rate of oceanic overturn. The processes that remove refractory deepwater DOC, the most abundant form of organic matter in the modern ocean, remain a major challenge in understanding the global carbon cycle (Hansell *et al.*, 2009; Jiao *et al.*, 2010). DOC on continental margins is mixed with continentally-derived DOC that has a different composition from marine-derived DOC (Bauer, 2002), but the same general trends in concentration and radiocarbon age with depth occur as in the open ocean (Bauer & Druffel, 1998).

## DYNAMICS OF THE NEOPROTEROZOIC DOC POOL

The size of the modern DOC pool makes it important in the global carbon cycle, and in recent years it has been hypothesized that it played an even larger role in the Precambrian. An analysis of Neoproterozoic carbon isotope records led Rothman *et al.* (2003) to suggest that these records are inconsistent with a conventional steady-state carbon-cycle model. Instead, they argued that the isotope dynamics are best explained by the presence of two large pools of ocean carbon, one  $\text{CO}_2$  and one DOC. Their modeling suggested that DOC levels were 2–3 orders of magnitude greater than those in the modern or Cenozoic oceans. Build-up of this large DOC pool, as inferred from the onset of decoupling between the organic and inorganic carbon isotope records, is currently constrained to after the Sturtian glaciation at  $\sim 720\ \text{Ma}$  (Swanson-Hysell *et al.*, 2010). Although the oxidation of this DOC pool has been invoked to explain extremely large-magnitude carbonate carbon isotope excursions in the Ediacaran, such as the Shuram anomaly (Fike *et al.*, 2006), Bristow & Kennedy (2008) have shown that the levels of either sulfate, oxygen, or both, present on the Ediacaran earth

are unlikely to have sustained an excursion such as the Shuram anomaly for its presumed duration by oxidation of the DOC pool alone, and this is assuming that the Shuram anomaly is even reflective of the oceanic carbon cycle (Knauth & Kennedy, 2009; Derry, 2010).

Here, rather than using geochemistry to directly infer carbon cycle processes, we use instead the paleoecology of the Mistaken Point biota to make inferences regarding DOC in the Ediacaran ocean. It should be noted that many studies considering the possibility of a large Neoproterozoic DOC pool (e.g., Fike *et al.*, 2006; Swanson-Hysell *et al.*, 2010) include true DOC ( $<0.2\ \mu\text{M}$ ), suspended colloidal matter and fine particulate organic carbon under the term DOC. Thus, the arguments for a “DOC”-rich deep ocean in the Proterozoic are difficult to directly compare to the modern oceanography literature on which the following discussion is based, and arguments regarding labile DOC for adsorptive feeding by eukaryotes should be considered at least partly distinct from geochemical arguments for an ocean with a large organic carbon pool.

The depth at which the rangeomorphs likely lived is, like most paleo-depth inferences, difficult to precisely constrain. Rangeomorphs from Avalon are preserved entirely *in situ* (Seilacher, 1999; Clapham *et al.*, 2003; Wood *et al.*, 2003) and thus sedimentary features can be used to constrain their depth. All available sedimentary features imply that the sediments were deposited below storm wave base (Myrow, 1995; Wood *et al.*, 2003; Ichaso *et al.*, 2007). Yet this represents a very conservative minimum estimate. The Mall Bay, Drook and Briscal Formations are interpreted as part of a basin-floor, axial turbidite system, and the Mistaken Point and Trepassey Formations are interpreted as a toe-of-slope environment dominated by contourite and turbidite deposition (Wood *et al.*, 2003). The fossils are found in a stratigraphic succession consisting of  $\sim 5$  kilometers of uninterrupted turbiditic sediments, with the first evidence of wave-generated structures in the Signal Hill Group, more than 1 kilometer higher in the succession than the Mistaken Point Formation and nearly 3 km above the lowest rangeomorphs in the Drook Formation. Despite the numerous sea-level oscillations that must have occurred over the  $\sim 15$  Myr of ice-house deposition, no evidence of storms or exposure is present. These paleoenvironments, combined with the thickness of deep-water strata, implies depths on the order of several hundred to thousands of meters (Wood *et al.*, 2003; Ichaso *et al.*, 2007). Similar taxa of rangeomorph fossils also occur in the Ediacaran Sheepbed Formation in the Mackenzie Mountains, Northwest Territories, Canada (G.M. Narbonne and M. Laflamme, in prep.), where both the shelf margin and the slope angle can be determined, and basin reconstruction allows more precise depth estimates of  $\sim 1\text{--}1.5$  kilometers (Dalrymple & Narbonne, 1996).

These depths are well below that at which “labile” DOC is present in the modern ocean. Radiocarbon ages (Williams

& Druffel, 1987; Bauer *et al.*, 1992), DOC concentration profiles (Hansell & Carlson, 1998) and degradation experiments (Barber, 1968) indicate that DOC below several hundred meters in the modern ocean is old, refractory and resistant to further microbial decay. This deep, refractory DOC may be so resistant to biological consumption that its removal requires abiotic processes such as photochemical breakdown as the deep DOC cycles back to the surface (Kieber *et al.*, 1989; Mopper *et al.*, 1991; Benner & Biddanda, 1998), or adsorption on to suspended particles (Druffel *et al.*, 1992). Long-term batch reactor decay experiments on surface-derived DOC also support the hypothesis that the labile fraction is used on a timescale of days, and the remaining refractory fraction is stable against microbial decay on a timescale of years (Ogura, 1972; Fry *et al.*, 1996; Ogawa *et al.*, 2001). Given the extremely refractory nature of modern deep-ocean DOC and its extreme nitrogen and phosphorous depletion, it seems unlikely (although as of yet untested) that eukaryotic organisms such as those living at Mistaken Point could obtain the majority of their nutrition from such a source, no matter how abundant. Two possibilities exist that could explain the apparent anomaly of DOC feeding among the Mistaken Point biota despite living at great depths.

#### Preservation of labile DOC in a dysoxic/anoxic deep ocean

First, because the Neoproterozoic ocean is widely agreed to be more reducing than the Phanerozoic ocean (reviewed by Lyons *et al.*, 2009), such conditions may have led to the preservation of labile DOC components in the water column. Although some oxygen was present in the water overlying the Mistaken Point biota (Canfield *et al.*, 2007), the iron speciation signature indicates dysoxic rather than fully oxygenated conditions. The Mistaken Point organisms may have lived in a “sweet spot” where the ocean provided enough oxygen to support eukaryotic life but not enough to degrade surface-produced labile DOC during its advective transport to depth. However, studies of amino acid degradation in modern Oxygen Minimum Zones (OMZ), a potential Proterozoic analog, do not support the hypothesis that reduced oxygen levels can protect labile DOC from biological utilization. In a vertical transect of the Chilean OMZ, Pantoja *et al.* (2009) found no appreciable difference in the concentration of dissolved free amino acids, total peptides (<3 kDa), or the percentage of amino acids and peptides relative to total DOC in the dysoxic OMZ core vs. the more oxygenated waters above and below. Additionally, they reported no obvious changes in rates of either tetra-alanine hydrolysis or leucine uptake through the vertical transect. This mirrors other studies demonstrating that labile DOC can be decomposed as rapidly under anoxic conditions as oxic, even in low-sulfate lake water that mimics the Proterozoic (Bastviken *et al.*, 2001). In other words, lower oxygen (or oxidant) levels will not prevent the degradation of the labile DOC fractions

produced in the surface ocean (where most new DOC is produced in the modern) during its transport to depth through advection.

#### Zooplankton and DOC

Instead, we hypothesize that the main factor keeping the Ediacaran deep ocean swathed in labile DOC was the lack of metazoan zooplankton. The advent of metazoan zooplankton likely occurred in the approximately Tommotian (Early Cambrian – Butterfield, 1997), and brought about two changes that impacted the distribution of labile DOC in the ocean. The first was the conversion of a large percentage of primary productivity into labile DOC in the surface ocean, which was then recycled through the microbial loop (Azam *et al.*, 1983; Pomeroy *et al.*, 2007); the second was through the reorganization of organic carbon export. With respect to the first change, quantitative studies suggest that more than half of DOC in the modern ocean is produced by protozoan and metazoan zooplankton (Jumars *et al.*, 1989; Strom *et al.*, 1997; Nagata, 2000). This occurs through sloppy feeding and egestion (Moller *et al.*, 2003) and accidental physical fragmentation of marine snow (Goldthwait *et al.*, 2005). DOC is also produced as mucus from gelatinous zooplankton (Hansson and Norrman, 1995). The DOC produced by zooplankton is not only abundant, but extremely labile and capable of fueling dramatically increased bacterial production relative to non-zooplankton controls (Strom *et al.*, 1997; Kragh & Sondergaard, 2004; Kragh *et al.*, 2006; Condon *et al.*, 2010). Zooplankton may contribute disproportionately to the labile DOC pool in the surface ocean; Condon *et al.* (2010), for instance, found that ctenophores in Chesapeake Bay contributed <1% day<sup>-1</sup> to the bulk DOC pool, but 18–29% day<sup>-1</sup> to the labile pool. Given the ecological feedbacks associated with the introduction of metazoan zooplankton (Butterfield, 2009), the assumption that their effects can be quantitatively subtracted from the modern DOC cycle to obtain a picture of the Neoproterozoic is almost certainly simplistic, but at a first order, the absence of metazoan zooplankton would likely result in less labile DOC produced in the surface ocean and a higher percentage of fresh, intact primary productivity exported to the deeper ocean from the surface ocean.

The second impact of metazoan zooplankton, the reorganization of organic carbon export, is primarily caused by the advent of metazoan fecal pellets (Logan *et al.*, 1995) and the evolution of large, export-prone algae (Butterfield, 2009). In the Precambrian, export of primary production was presumably affected by physical aggregation into marine snow, which remains the major export pathway in the modern ocean (Turner, 2002). As Proterozoic primary productivity was dominated by bacterial phototrophs (Johnston *et al.*, 2010), the sinking rate of this marine snow would have been much slower than in Phanerozoic, due to the small initial size of

bacterial cells (sinking rate is related to size – Burd & Jackson, 2009). The lack of biomineralized ballast from diatoms and coccoliths would also have reduced sinking rates. Thus, in the Ediacaran, small slowly-sinking aggregates of bacterial phototrophs were extensively re-worked on their descent to the seafloor. During sinking, organic matter was, in part, converted into labile DOC through solubilization (e.g., Smith *et al.*, 1992) or bacterial/viral lysis. In other words, slowly sinking Ediacaran marine snow smeared out the depth at which labile DOC was produced, and this labile DOC released at depth could then be used by deeper-water osmotrophs such as at Mistaken Point.

The rise of metazoan zooplankton resulted in an increase in the rate of organic carbon transport to the sediment. This occurred through the introduction of macrozooplankton fecal pellets, which can sink rapidly, in contrast to those of smaller plankton (Turner, 2002). The advent of large, rapidly sinking eukaryotic algae, which may have evolved in response to zooplankton grazing pressures (Butterfield, 2009) would have also significantly increased the speed of export. Thus, in the Phanerozoic oceans, primary productivity is either converted to DOC near the ocean surface and recycled through the microbial loop, or shuttled with relative rapidity to the seafloor, where it is incorporated into the sediments by bioturbating organisms and removed from the system. Consequently, there is little labile DOC at depth, in contrast to what is envisioned for the Ediacaran, where the production of new, labile DOC at depth from slowly sinking marine snow could support biological communities subsisting almost entirely on this resource.

## CONCLUSIONS AND FUTURE DIRECTIONS

The classic Ediacaran Mistaken Point fauna of Newfoundland appears to contain two groups of organisms, rangeomorphs and sponges (represented by *Thectardis*), that likely received much of their nutrition from DOC. The presence of osmotrophs living in the deep ocean (using the sedimentologists' definition of several hundred meters depth or more) presents a paradox: modern deep-ocean DOC is old, refractory, nitrogen- and phosphorous-depleted, and essentially biologically inert. The paleoecology of the Mistaken Point biota indicates non-uniformitarian DOC dynamics, which permitted a much higher percentage of labile DOC to reach the deep ocean. This may have been due to more reducing ocean conditions, but more likely reflects the absence of metazoan zooplankton grazers. The reduction in labile DOC at depth, whatever the cause, was likely instrumental in the decline of the rangeomorphs (Sperling *et al.*, 2007). In contrast to sponges, which have a mixotrophic diet and can actively pump water through their bodies, allowing them to inhabit the deep ocean in the modern, rangeomorphs were passive feeders, and likely almost totally dependent on labile DOC. We hypothesize that the reduction of this labile deep-ocean DOC

resulted in the decline and eventual extinction of the rangeomorph faunas.

Around 97% of organic carbon in the modern ocean is the dissolved pool, and changes in the size and composition of this pool influences a diverse range of processes from the base of the food chain (the microbial loop) to atmospheric CO<sub>2</sub> levels. Modern studies provide useful analogs, but their utility to explain Precambrian ocean conditions may be limited – indeed almost every DOC production and removal mechanism in the modern ocean (Nagata, 2000; Carlson, 2002) would have operated differently given current understanding of Neoproterozoic geobiology. Fundamental questions remain that can be addressed by researchers using mesocosm techniques to replicate Proterozoic conditions, such as the dynamics of DOC production during the sinking of marine snow in cyanobacteria-dominated systems lacking fecal pellets or biomineralized ballast. The relationship between more labile forms of DOC and oxidant levels also needs to be addressed, particularly as causal hypotheses for large negative carbon isotope excursions by oxidation of a DOC pool (Rothman *et al.*, 2003; Fike *et al.*, 2006; Sperling *et al.*, 2007; McFadden *et al.*, 2008) require not only the build-up of a large DOC pool, but of a pool that is at least ultimately biologically-utilizable. Biological utilization of the recalcitrant DOC characterizing the modern deep ocean is not limited by oxidant levels but by the nature of the substrate. Much remains to be investigated regarding the relationship between the large negative isotope excursions and the DOC pool, the precise timing of the provenance shift in sedimentary hydrocarbons (Logan *et al.*, 1995), and the redox structure of the Neoproterozoic ocean. Understanding the dynamics of the DOC pool, by far the largest pool of organic carbon in the ocean, is crucial to understanding the geobiology of the Neoproterozoic, and represents an area of inquiry, utilizing a diverse range of data from carbon isotope records to the paleoecology of a largely extinct community, that is perfectly suited to the interdisciplinary nature of the field.

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