

# **Constructional and functional anatomy of Ediacaran rangeomorphs**

Running head: **Rangeomorph construction and functional anatomy**

**Nicholas J. Butterfield**

**Department of Earth Sciences**

**University of Cambridge**

**Cambridge, UK CB2 3EQ**

email: **[njb1005@cam.ac.uk](mailto:njb1005@cam.ac.uk)**

## Abstract

Ediacaran rangeomorphs were the first substantially macroscopic organisms to appear in the fossil record, but their underlying biology remains problematic. Although demonstrably heterotrophic, their current interpretation as osmotrophic consumers of dissolved organic carbon (DOC) is incompatible with the inertial ( $> Re$ ) and advective ( $> Pe$ ) fluid-dynamics accompanying macroscopic length-scales. The key to resolving rangeomorph feeding and physiology lies in their underlying construction. Taphonomic analysis of three-dimensionally preserved *Charnia* from the White Sea identifies the presence of large, originally water-filled compartments that served both as a hydrostatic exoskeleton and semi-isolated digestion chambers capable of processing recalcitrant substrates – likely in conjunction with a resident microbiome. At the same time, the hydrodynamically exposed outer surface of macroscopic rangeomorphs would have dramatically enhanced both gas exchange and food delivery. A bag-like epithelium filled with transiently circulated seawater offers an exceptionally efficient means of constructing a simple, DOC-consuming, multicellular heterotroph. Such a bodyplan is broadly comparable to that of anthozoan cnidarians – minus such derived features as muscle, tentacles and a centralized mouth. Along with other early bag-like fossils, rangeomorphs can be reliably identified as total-group eumetazoans, potentially colonial stem-group cnidarians.

Key words: Neoproterozoic, Eumetazoa, external digestion, hydrodynamics, hydrostatic exoskeleton, microbiome, taphonomy

## Introduction

Rangeomorphs were conspicuous members of the Ediacaran biosphere, present from roughly the end of the Gaskiers glaciation through to the beginning of the Cambrian (~575–540 Ma). As the first substantial instances of large complex organisms in the fossil record they mark a key transition in geobiological history, presaging the first appearance of unambiguous animals at ~555 Ma. Even so, there is little consensus on the phylogenetic affiliations of rangeomorphs, with interpretations ranging from total-group cnidarians, ctenophores or sponges to stem-group (eu)metazoans – or possibly an entirely unrelated lineage of multicellular/macrosopic eukaryotes (Xiao & Laflamme, 2009). The problem with these particular fossils is not just their taxonomic placement, however, but a fundamentally deeper lack of understanding of how they were constructed, and how they worked as organisms.

Physiologically, macroscopic/multicellular organisms work in much the same way as their microscopic/unicellular counterparts, but with the added allometric challenges of conveying resources to internalized tissues and supporting the associated mass. Because of the fundamental reductions of surface area to volume (SA:V) that accompany increased body size, the evolution of large three-dimensional organisms necessarily involved major anatomical innovations. Even at modern levels of oxygen, for example, the maximum diameter of aerobic organisms lacking some sort of differentiated circulatory or respiratory apparatus is less than 2 mm (Catling et al., 2005). There are, however, significant advantages to large body size, not least environmental buffering, systematic decreases in mass-specific metabolic demand (Glazier, 2006; DeLong et al., 2010), and the emergence of scale-dependent mechanical, chemical and hydrodynamic properties (Sebens, 1987; Koehl, 1996; Hurd, 2000; Solari, Kessler & Goldstein, 2007; Guizien & Ghisalberti, 2016). Simply as a consequence of length-scale ( $L$ ) and background fluid velocity ( $U$ ), for example, large organisms operate in a world of elevated Reynolds numbers where movement is dominated

by inertial rather than viscous forces ( $Re = UL/v$ ), and at elevated Péclet numbers where material exchange is dominated by advection rather than molecular diffusion ( $Pe = UL/D$ ) ( $v$  = kinematic viscosity;  $D$  = rate of diffusion). Such dynamics offer fundamentally enhanced levels of motility, feeding, and gas exchange to macroscopic organisms (Butterfield 2018) – provided the underlying issues of construction and resource distribution can be addressed.

Rangeomorphs are characterized by a broadly frond-like habit, built around a cm-scale branching element that exhibits self-similarity over three or four ‘pseudo-fractal’ levels (Narbonne, 2004; Brasier, Antcliffe & Liu, 2012; Hoyal Cuthill & Conway Morris, 2014). Various arrangements of these elements, often in concert with basal holdfasts, elevating stalks or interconnecting rods, gave rise to a significant range of larger scale forms including: bi-terminal recliners (e.g., *Fractofusus*), unstalked unifoliate fronds (e.g., *Charnia*), stalked unifoliate fronds (e.g., *Avalofractus*), unstalked multifoliate fronds (e.g., *Bradgatia*), stalked multifoliate fronds (e.g., *Rangea*), and compound fronds (e.g., *Hapsidophyllas*) (Fig. 1). Although originally interpreted as macroscopic algae (Ford, 1958), the abundant *in situ* preservation of rangeomorphs in deeper-water strata of Avalonia has convincingly ruled out a photosynthetic habit (Wood et al., 2003). And although some forms look superficially like modern sea-pens, their distinct styles of construction and growth rule out any direct affiliation to extant octocoral cnidarians (Seilacher, 1989; Antcliffe & Brasier, 2007).

Because of their anchored and generally elevated habit, rangeomorphs have traditionally been interpreted as microphagous suspension feeders, ecologically analogous to sponges or anthozoan cnidarians (Jenkins, 1985). Unlike these living forms, however, rangeomorphs appear to lack tentacles, openings or any other feeding-related features, even in specimens preserving detail on a scale of tens of micrometres (Narbonne, 2004). As such, it has been widely assumed that nutrient uptake took place on the outside of the organism, after the manner of osmotrophic bacteria or fungi (McMenamin, 1993; Laflamme, Xiao &

Kowalewski, 2009; Sperling, Peterson & Laflamme, 2011). Certainly the characteristic ‘fractal’ branching would have increased the proportion of exposed surface area on which this might have occurred, but it remains to be demonstrated that rangeomorphs could actually feed in this fashion (Liu, Kenchington & Mitchell, 2015).

### **Osmotrophy and DOC – a primer**

The most immediate issue arising from the osmotrophy model for rangeomorphs is the imprecise, often inconsistent use of the term itself. In its most general sense, osmotrophy is simply the process by which dissolved substrates are passed across cell membranes (Jumars et al., 1993; Karp-Boss, Boss & Jumars, 1996; Thingstad et al., 2005). At least implicitly, it is limited to external, environmentally exposed surfaces, which usefully distinguishes it from otherwise similar processes of internalized uptake (e.g., in eumetazoan guts and the food vacuoles of phagocytizing protozoans). The textbook exemplars of osmotrophic feeding – heterotrophic prokaryotes and fungi – are also ‘external digesters,’ where organisms actively excrete hydrolytic enzymes and recover the digested products. There are risks to this type of feeding however, most obviously through the dispersive loss of exo-enzymes and product in aqueous environments, but also their exploitation by unrelated or non-contributing organisms (Jumars et al., 1993; Karp-Boss, Boss & Jumars, 1996; Vetter et al., 1998; Arnosti, 2011; Richards & Talbot, 2013). The key to limiting such losses is containment. Fungi typically manage this through the penetration of solid substrates, whereas osmotrophic prokaryotes exploit the viscosity-dominated fluid dynamics associated with small length scales ( $\ll Re$ ). The diffusive boundary layer (DBL) surrounding micrometre- and sub-micrometre-sized cells is effectively impervious to advective loss, greatly facilitating the rate-limiting steps of both hydrolytic digestion and trans-membrane uptake (Jumars et al., 1993; Langlois et al., 2009; Arnosti, 2011). Conversely, the DBL and its facilitation of external digestion/osmotrophy are

progressively eroded at larger length scales. Indeed, the primary impediment to osmotrophic feeding in large organisms is not SA:V *per se*, but the challenge of digesting and incorporating substrate under elevated *Re* conditions.

The discussion of osmotrophy has been further confused by the term ‘dissolved organic carbon’ (DOC), the substrate on which rangeomorphs are assumed to have fed. Despite early proposals to limit the term to genuinely soluble components (Sharp, 1973), DOC has come to be defined operationally as the reduced carbon content of a filtered water sample – with the pore-size of the filter ranging more or less arbitrarily from 0.2 to 1.0  $\mu\text{m}$  (Verdugo et al., 2004). As such, DOC now includes a disparate range of materials, from fully dissolved molecules to colloids, gels, viruses, and even small microbes.

Further classification of DOC is based on environmental longevity – on the one hand ‘labile DOC’ with residence times of hours to days, and on the other ‘recalcitrant DOC’ which persists from weeks to tens of thousands of years (Hansell, 2013; Follett et al., 2014). In structural terms, labile DOC is represented by free monomers and small oligomers (< 600 daltons) and is the only fraction available for direct osmotrophic uptake. Unsurprisingly, it has limited potential for environmental accumulation, with amino acids and sugars in the modern ocean occurring at concentrations of less than a billionth of a gram per litre (Hansell, 2013; Moran et al., 2016). By contrast, the larger molecules and materials comprising recalcitrant DOC accumulate substantially in the oceans, collectively representing more than 200 times the carbon present in marine biomass. Even so, DOC remains conspicuously dilute in marine environments ( $\sim 34$  to  $> 80 \mu\text{mol kg}^{-1}$ ), often falling below the threshold necessary to sustain microbially mediated hydrolysis (Arrieta et al., 2015). This alone may contribute to its extended residence time.

There are multiple sinks for recalcitrant DOC in the modern oceans, including both biological remineralization and sedimentary adhesion/burial. Of the former, a substantial

fraction ends up being captured and consumed by suspension-feeding animals. Benthic sponges, for example, have an extraordinary capacity to extract colloidal DOC from large volumes of water (Yahel et al., 2003; de Goeij et al., 2013; Kahn et al., 2015), a habit emulated in the pelagic realm by actively swimming salps and tunicates (Flood, Deibel & Morris, 1992; Sutherland, Madin & Stocker, 2010). None of these ‘DOC feeders’ can be considered osmotrophic however, since all of the associated digestion and uptake takes place internally – by endocytic choanocytes in the case of sponges (Leys & Eerkes-Medrano, 2006) and within a differentiated gut in tunicates and other eumetazoans (e.g., Dishaw et al., 2014). At the same time, there is a proportion of DOC that physically aggregates to produce larger ‘particulate organic carbon’ (POC), with the resulting flakes, gels and transparent exopolymer particles (TEP) available for consumption via conventional eumetazoan-grade capture and ingestion (Camilleri & Ribí, 1986; Verdugo et al., 2004; Mari et al., 2017).

Despite these various non-osmotrophic means of incorporating DOC, it is clear that a range of aquatic eukaryotes do exploit it directly. Labelling experiments, for example, have demonstrated the osmotrophic uptake of acetate, monosaccharides, amino acids and fatty acids by most major invertebrate clades (Wright & Manahan, 1989; Baines, Fisher & Cole, 2005; Skikne, Sherlock & Robison, 2009; Gori et al., 2014; Blewett & Goss, 2017). There are also reports of uncharacterized DOC uptake (e.g., Roditi, Fisher & Sanudo-Wilhelmy, 2000; Barnard et al., 2006; Rengefors et al., 2008), though it is notable that these substrates were all derived from fresh algal or arthropod lysates. In other words, the osmotrophy observed in modern eukaryotes and metazoans appears to be limited exclusively to the labile, low molecular-weight DOC that requires no prior digestion – and even then, uptake rates are typically 2–4 orders of magnitude lower than that of corresponding internal feeding (Wright & Manahan, 1989). Reports of aquatic invertebrates feeding osmotrophically on recalcitrant DOC (e.g., Mcmeans et al., 2015) are likely to involve microbial intermediaries or other

means of repackaging leading to internalized digestion (e.g., Camilleri & Ribí, 1986; Höss et al., 2001; Eckert & Pernthaler, 2014).

Whatever the absolute quality or quantity of food, it only becomes metabolically available once it has been translocated from the external environment into a cell. Although  $O_2$ ,  $CO_2$  and a variety of small hydrophobic molecules diffuse more or less freely across phospholipid cell membranes, most organic molecules – including amino acids and monosaccharides – can only be taken up via membrane-embedded transporter proteins. As such, maximum uptake rates are determined by the density and specificity of transporters, and the non-trivial time required for substrate exchange (Confer & Logan, 1991; Karp-Boss, Boss & Jumars, 1996). Glucose and amino acid transporters, for example, will saturate under elevated substrate concentrations, limiting the utility of locally enhanced delivery. Even so, the vanishingly low concentrations of free monomers in the modern ocean means that the rate-limiting step for marine osmotrophy will almost always revert to the hydrolytic digestion of more recalcitrant DOC (Confer & Logan, 1991; Moran et al., 2016) – a process fundamentally at odds with fluid dynamics at macroscopic length scales.

Ultimately, of course, the challenge for all heterotrophic organisms is accessing food. For microbes operating under low  $Re$  and  $Pe$  regimes, the presence of a thick, essentially permanent DBL means that substrate delivery is dominated by molecular diffusion (Karp-Boss, Boss & Jumars, 1996). Despite their extraordinary capacity to digest recalcitrant DOC, the physical inability of osmotrophic microbes to pump or swim substantially through water means they are prone to starvation under oligotrophic conditions (Arrieta et al., 2015). Delivery can be dramatically enhanced in larger organisms simply through the accompanying inertial and turbulent fluid dynamics (Langlois et al., 2009; Singer, Plotnik & Laflamme, 2012; Ghisalberti et al., 2014; Guizien & Ghisalberti, 2016; Butterfield, 2018;), but at the cost of eroding the stable DBL necessary for external digestion (Vetter et al., 1998; Arnosti,

2011; Richards & Talbot, 2013). In principle, then, macroscopic heterotrophs should be able to make a living under fundamentally more oligotrophic conditions than their microbial counterparts (Ghisalberti et al., 2014), but only if there is an alternative means of digesting recalcitrant food.

### **Osmotrophic Rangeomorphs?**

Laflamme et al. (2009) have argued that Ediacaran rangeomorphs fed osmotrophically via their ‘fractally’ enhanced SA:V properties, noting a marginal overlap with some exceptionally large living prokaryotes. There are problems with this study however, not least the choice of modern analogues. Of the eight ‘strictly osmotrophic megabacteria’ included in the analysis, only one is actually a free-living osmotroph – the relatively modest-sized (<15 µm diameter) archaeon *Staphylothermus marinus*. Two others are substantially larger, but known exclusively from the guts of aquatic vertebrates (*Sporospirillum praeclarum* in tadpoles and *Epulopiscium fishelsoni* in surgeon fish), where neither substrate digestion nor advective loss are relevant factors. None of the remaining five taxa is osmotrophic, or even heterotrophic: *Thiomargarita*, *Achromatium*, *Beggiatoa*, and *Thiovulum* are all sulfur-oxidizing chemoautotrophs, and *Prochloron* is a photoautotroph. Indeed, the most likely explanation for the exceptionally large dimensions of these primary producers is the advective delivery of (freely diffusible) CO<sub>2</sub> at larger length scales. In any event, there are no extant heterotrophic prokaryotes, free-living or otherwise, that fall within the calculated SA:V range of Ediacaran rangeomorphs .

The likelihood of osmotrophic feeding in rangeomorphs is also problematic in terms of metabolically available DOC. Although the Proterozoic oceans might well have contained high concentrations of total DOC (e.g., Shields, 2017), any substantial accumulations would have been chemically recalcitrant and unavailable for direct osmotrophic uptake. Arguments

for the presence of abundant *labile* DOC in Proterozoic oceans – due to the absence of metazoan zooplankton and concomitant slow sinking of phytoplankton (Sperling, Peterson & Laflamme, 2011) – are incompatible with the voracious consumption of free monomers by heterotrophic microbes, particularly in well-oxygenated surface-waters where almost all labile DOC is produced. Labile DOC might well have been intermittently elevated in the vicinity of Ediacaran rangeomorphs (Budd & Jensen, 2017), but never at the continuously concentrated levels enjoyed by modern gut-dwelling Bacteria (cf., Pollak & Montgomery, 1994; Schulz & Jørgensen, 2001).

The most direct means of resolving the trade-off between effective food delivery (enhanced in larger organisms and elevated  $Re$ ) and its digestion/incorporation (enhanced at low  $Re$ ) is to separate the two processes. At a unicellular level, the contained intracellular digestion of DOC/POC by phagocytizing protists by-passes many of the fluid-dynamic challenges faced by osmotrophic prokaryotes, though new ones inevitably arise; e.g., the elevated  $Re$ /turbulence accompanying larger eukaryotic cells and its interference with prey *capture* (Dolan et al., 2003). At multicellular/macrosopic length-scales even phagocytosis becomes hydrodynamically untenable without anatomical or behavioural adaptations for attenuating flow; e.g., the ramifying aquiferous system of sponges (Leys & Eerkes-Medrano, 2006), the enveloping habit of placozoans (Smith, Pivovarova & Reese, 2015), and the chambered, often channelized gastrodermal system of cnidarians (Southward, 1955; Schick, 1991; Harmata et al., 2013; Raz-Bahat et al., 2017; Goldberg, 2018; Steinmetz 2019). Such dynamics presumably account for the exclusively gastrodermal uptake of zooxanthellae in photoendosymbiotic anthozoans. In the case of rangeomorphs, furrows associated with the ‘fractally’ divided integument offer the only potential for comparable levels of isolation on the external surface – though these notably constitute just a fraction of the total surface area.

What the macroscopic size of rangeomorphs certainly does confer is elevated Reynolds and Peclet numbers. Ghisalberti et al. (2014) presciently recognized the fluid dynamic implications of large size in Ediacaran macrofossils, noting that the turbulence generated by the interaction of physical currents and an elevated macro-benthos comprehensively overrides any diffusional limits on the delivery of dissolved and suspended resources. Although problematic in terms of osmotrophic feeding, such ‘canopy effects’ are directly applicable to freely diffusible O<sub>2</sub> and CO<sub>2</sub>; indeed, all three of the datasets used by Ghisalberti et al. (2014, figs. 3 and S2) to illustrate this principle were specifically measures of oxygen transport. In this light, the most immediate advantage to rangeomorphs adopting a macroscopic habit was access to advective food delivery and gas exchange (Singer, Plotnik & Laflamme, 2012). Additional ventilatory effects will have been generated by ciliated epithelia, allowing rangeomorphs to employ their external surface as a breathing device under both high-energy and relatively stagnant physical flow (cf., Short et al., 2006; Shapiro et al., 2014; Cavalier-Smith, 2017; Dufour & McIlroy, 2017).

### **The rangeomorph skeleton**

Whatever the particular habits of Ediacaran macrofossils, they were clearly supported by some sort of skeletal superstructure, an anatomical feature that is likely to illuminate other aspects of their biology. In the absence of obvious biomineralization, this has been widely envisaged as a hydrostatic endoskeleton, comparable to the coelomic system of annelid worms (Runnegar, 1982), the syncytia of giant ‘unicellular’ protists (Seilacher, 1989; Seilacher, 1992; Seilacher, Grazhdankin & Legouta, 2003) or a sponge-grade mesenchyme-like mass (Dufour & McIlroy, 2017). More generally, Laflamme et al. (2009) have argued that ‘much of the internal body cavity... may have been filled by metabolically inactive material (inorganic, organic, or fluid).’

The key to resolving the nature of the rangeomorph skeleton lies in its taphonomic dissection. Although most rangeomorphs are preserved as more or less two-dimensional bedding-plane imprints – a product of felling, degradational collapse and early diagenetic ‘death-mask’ cementation – there is a notable subset of specimens that have been preserved as conspicuously three-dimensional casts and moulds (Jenkins, 1985; Fedonkin, 1994; Dzik, 2002; Grazhdankin & Seilacher, 2005; Vickers-Rich et al., 2013; Sharp et al., 2017). Such sedimentary infilling points to the presence not only of large internalized chambers, but also chamber walls of sufficient integrity to act as the containing form. In *Charnia* specimens from the Winter Mountains of the White Sea, for example, substantial parts of the fronds have been infilled with silt early and rapidly enough to capture their full three-dimensional profile (Fedonkin, 1994; Grazhdankin, 2004; Dunn et al., 2018), even as adjacent unfilled areas collapsed to yield a more typical two-dimensional death-mask (Fig. 2).

Casting is a common mode of preservation in biomineralized or heavily lignified organisms, but is less expected in ‘soft-bodied’ Ediacaran forms (Seilacher, 1970; Rex, 1985; Retallack, 1994; Maeda et al., 2010). Where it does occur, the process will be similarly dependent on chambers with self-supporting walls, but proceeding on fundamentally shorter timescales. Given the rapidly collapsing two-dimensional habit of rangeomorphs in general, it follows that the original contents of the chambers must have been correspondingly fluid. The effectively instantaneous casting of *Charnia* compartments (Fig. 2) is inconsistent with the original contents having the viscosity of syncytial cytoplasm (cf., Seilacher, 1989; Seilacher, 1992), mesenchyme (cf., Dufour & McIlroy, 2017), or coelomic fluids (cf., Runnegar, 1982), particularly given the rapid wound-repair systems associated with these fully isolated hydrostatic skeletons (e.g., Menzel, 1988; Duckworth, 2003; Kamran et al., 2017). By far the most likely material filling the compartments of rangeomorphs – and conferring their primary skeletal support – is locally contained low-viscosity seawater.

In the absence of obvious openings in the body wall (Narbonne, 2004), the route by which such water entered rangeomorph chambers has yet to be identified. One likely possibility is that the conduits were simply too small or ephemeral to fossilize under the associated taphonomic regimes. Even with the fundamentally greater levels resolution seen in ‘Burgess Shale-type preservation,’ for example, the ostia and associated aquiferous system of sponges have never been directly preserved (Butterfield, 2003). The external openings of water-pumping siphonozooids in colonial octocorals can be similarly cryptic, even in living specimens (Fig. 3d) (Hickson, 1883; Brafield, 1969; Williams, Hoeksema & Van Ofwegen, 2012; Nonaka et al., 2012), and it is notable that even the mm-sized siphonozooids of pennatulaceans fail to preserve under optimized laboratory burial conditions (Norris, 1989).

Insofar as such features are only expected under the most exceptional taphonomic circumstances, it is worth revisiting Grazhdankin’s (2004) original documentation of the 3D Winter Mountains *Charnia*. Intriguingly, the upward-facing surfaces of at least two specimens bear serially repeated lensoid structures (Fig. 2a, e, arrows) that are not preserved in corresponding 2D fossils. The continuity of fossil-casting silt through these mm-sized structures (Fig. 2c, arrows) points to their likely function as anatomical conduits connecting the internal chambers to surrounding seawater. Taphonomic merger of the ‘upper’ and ‘lower’ surfaces during more typical death-mask preservation readily accounts for their absence in most *Charnia* fossils (Fig. 4c, d) – as well as the misleading impression that the two sides of *Charnia* fronds were morphologically identical (cf., Dunn et al. 2018). Indeed, the preservation of original spatial relationships in these exceptional specimens demonstrates that much of the underlying ‘fractal’ architecture was associated exclusively with the ‘lower’ surface (Fig. 2a, b). In view of their conspicuously mouldic expression, the ‘third-order branches’ of *Charnia* appear not to define external morphology, but rather mesentery-like structures with a primary purpose in expanding internalized surface area (Fig. 4).

Whether or not the serially repeated lensoid structures represent biological openings in the *Charnia* integument, it is unlikely that they provided the primary conduit for the infilling sediment. Comparable structures are not recorded in similarly preserved *Rangaea* specimens (e.g., Jenkins, 1985; Grazhdankin & Seilacher 2005; Vickers-Rich et al. 2013; Sharp et al., 2017), and such openings are almost universally guarded by ciliated and/or contractile cells in living organisms. Full three-dimensional preservation also requires sufficient ‘draft-through’ flow to deliver the casting sediment prior to degradational collapse (cf., Seilacher, 1970; Rex, 1985; Maeda et al., 2010), suggesting substantially larger-scale access to the internalized chambers. Given the high-energy tempestite conditions under which the Winter Mountains *Charnia* were buried (Grazhdankin 2004), the most likely avenue for of silt-entraining currents would have been through abrasive breaches in the thin body wall (cf., Bettignies, Thomsen & Wernberg, 2012). Indeed, parts of the upper surface of PIN 3993-7018 have clearly been eroded and amalgamated with contemporaneous cross-laminated silts (Fig. 2d); it is only where the castings are locally overlain by low-energy muddy laminae that the differentiated anatomy of this surface is preserved (Figs. 2a, e; 4c). In a similar vein, Brasier et al. (2013) have interpreted features of the high-relief rangeomorphs at Spaniard’s Bay as the consequence of body-wall rupture/removal during hydraulic scouring events, and it is notable that the majority of three-dimensionally cast rangeomorphs occur in conspicuously more abrasion- and transport-prone ‘Nama-type’ facies (Grazhdankin 2004; Grazhdankin & Seilacher, 2005; Vickers-Rich et al., 2013; Sharp et al., 2017).

Rapid sedimentary casting of bag-like compartments is also documented in a range of co-occurring non-rangeomorph Ediacaran taxa. Among the most spectacular examples are *in situ*, vertically oriented populations of *Charniodiscus* in Zimnie Gory sections of the White Sea (Grazhdankin, 2014; Ivantsov, 2016), reclined but similarly frondose *Pambikalbae* and

*Arborea* from Nilpena in South Australia (Jenkins & Nedin, 2007; Laflamme, Gehling & Droser, 2018; Dunn, Liu & Gehling, 2019; Droser et al. 2020), and globular tripartite *Ventogyrus* from the Onega River area of the White Sea (Ivantsov & Grazhdankin, 1997; Fedonkin & Ivantsov, 2007). All of these fossils have been variably infilled during event-bed sedimentation, yielding a taphonomic continuum from fully inflated three-dimensional casts through to essentially two-dimensional death-mask imprints. As with rangeomorphs, the form of the casts directly mirrors that of the external moulds, attesting to the thin deformable nature of the chamber walls (Jenkins & Nedin, 2007; Sharp et al., 2017) and the presence of a rapidly displaceable, chamber-filling fluid. Also like rangeomorphs, there is little direct evidence of the openings through which seawater may have entered in life – but similarly no expectation that these should be recognizably preserved. Again, the infilling sediment was most likely introduced via abrasional breaches in thin body-walls. Regardless of any phylogenetic connection to rangeomorphs, the localized 3D casting of these arboreomorphs and other problematica points to a similar grade of chambered construction and hydrostatic support.

### **Functional morphology of hydrostatic exoskeletons**

The recognition of rangeomorph chambers with direct conduits to the external environment means that the contained seawater was topologically on the outside of the organism – in other words, within a bag-like hydrostatic exoskeleton. There is nothing particularly exotic about such a system; indeed, it is the primary means of structural support among basal eumetazoans. In actinarian (sea anemones) and pennatulacean (sea pens/pansies) anthozoans, for example, it is transiently retained seawater in the gastrovascular system that provides the antagonist against which epithelial muscle acts to generate organism/colony form and movement (Fig. 3a) (Batham & Pantin 1950; Chapman, 1958). At a more

fundamental level, even the muscle can be dispensed with since the flow and containment of seawater within the system is based on embedded ciliary pumps/siphonoglyphs (Fig. 3c, d). This bag-like arrangement offers an exceptionally parsimonious means of constructing a multicellular macroscopic eukaryote – not based on costly biominerals, differentiated tissue systems or coelomic fluids, but on environmental water that comes for free. The only substantial costs are a mesoglea-like internal layer that defines the overall form of the inflated chamber (cf., Batham & Pantin, 1951; Tucker, Shibata & Blankenship, 2011), and an enveloping epithelial layer to ensure its integrity (Fig. 4a) (cf., Tyler, 2003; Jonusaite, Donini & Kelly, 2016). With a charging mechanism based on the plesiomorphic capacity of eukaryotes to pump water (Butterfield, 2018), such an apparatus provides access to most of the fluid dynamic advantages of large size without the metabolic trade-offs accompanying more complex, carbon-rich body plans (Thingstad et al., 2005; Acuña, López-Urrutia & Colin, 2011; Pitt et al., 2013).

Most significantly, the middle Ediacaran invention of this bag-like habit solved the problem of conducting extracellular digestion at macroscopic length scales. By containing the process within an essentially impermeable integument, hydrolytic exo-enzymes could now be freely released without advective loss to the environment or competing organisms, even under the turbulent conditions associated with centimetre to metre length-scales (cf., Sher et al., 2008; Agostini et al., 2012; Raz-Bahat et al., 2017; Goldberg, 2018; Steinmetz 2019). Combined with organismal control over the cycling of seawater, the presence of a large-scale holding and mixing vessel provided both the time and hydrodynamic conditions necessary for optimal uptake and digestion – particularly in the presence of substantially expanded mesentery-like surface area (Fig. 4a, b). In modern industrial applications such structures are known as chemical reactors; in biology they are regularly employed as guts (Penry & Jumars, 1987).

The most basic type of gut among living animals is the single-opening ‘batch reactor’ of predatory cnidarians, where individual prey items are processed within a (transiently closed) gastrovascular cavity, followed by the regurgitation of undigested remains (Schick, 1991; Sher et al., 2008; Schlesinger et al., 2009; Raz-Bahat et al., 2017; Steinmetz 2019). Such behaviour, however, is predicated on the availability of suitable prey, and a muscle-based means of capturing and manipulating it – for which there is no direct evidence in the middle Ediacaran. In this context, the more appropriate model for extracellular digestion is a ‘continuous-flow stirred-tank reactor’ (CSTR), involving the continuous processing of dissolved or suspended substrate as it passes through a reaction chamber (Penry & Jumars, 1986). This type of unidirectional water cycling is widely employed by extant cnidarians, where cilia- and siphonoglyph-based pumping is capable of marshalling complex flow-paths, even within blind-ended chambers and canals (Southward, 1955; Holley & Shelton, 1984; Schick, 1991; Parrin et al., 2010; Harmata et al., 2013; Goldberg, 2018). Fully open-ended unidirectional processing has also been achieved secondarily in colonial pennatulacean and alcyonacean octocorals, through the differentiation/interconnection of water-pumping siphonozooids and stolon systems (Fig. 3c, d) (Hickson, 1883; Brafield, 1969; Williams, Hoeksema & Van Ofwegen, 2012; Nonaka et al., 2012; ) – as well as in the atentaculate solitary coral *Leptoseris fragilis* via the formation of micrometre-scale gastrovascular pores (Schlichter, 1991). Significantly, active gastrovascular cycling of seawater proceeds even where its skeletal function has been largely superseded by hard skeleton, demonstrating a primary purpose in feeding and internal transport. The pseudo-fractally partitioned hydrostatic exoskeleton of rangeomorphs is similarly suited to such CSTR-like processing.

The Ediacaran introduction of large, gently stirred, semi-enclosed, reaction vessels would have been equally revolutionary from a microbial point of view. Along with the massively expanded area for surface attachment, microbial residence within the rangeomorph

chamber system offered both a continuously buffered habitat and essentially unlimited levels of host-delivered resources (Fig. 4b). At the same time, localized containment allowed the direct physiological coupling of otherwise incompatible modes of life. In the bilaterian gut, for example, it is clear that the anaerobic conditions necessary for optimal digestion are maintained both by and for the resident microbiome (Plante, 1990; Friedman et al., 2018; Litvak, Byndloss & Bäumler, 2018), even as the collective ‘holobiome’ takes advantage of a fully oxygenated existence. Comparably steep redox gradients are found in the gastrovascular cavities of extant cnidarians (Agostini et al., 2012), offering similar opportunities for such catabolic partnerships (Viver et al., 2017; Goldberg, 2018). In the case of actinarian and pennatulacean anthozoans, rhythmic cycling between hypoxic and anoxic conditions within the gastrovascular system (Brafield & Chapman, 1967; Chapman, 1972; Jones, Pickthall & Nesbitt, 1977; Brafield, 1980) reflects the active suppression of oxygen activity, even as oxygenated seawater is continuously shunted through the system, (Penry & Jumars, 1987; Smith & Waltman, 1995; Agostini et al., 2012). Given the ubiquity of metabolically diverse microbes in the marine realm, the Ediacaran appearance of bag-like rangeomorphs can be viewed as the original evolutionary experiment linking high-*Re* oxygen-respiring multicellular eukaryotes to a low-*Re*, hypoxic/anoxic microbial digester. Such symbioses will have dramatically expanded the capacity of Ediacaran eukaryotes to feed on dilute and/or recalcitrant DOC, while also tapping into the rich physiological, immunological and developmental potential of such redox-sensitive relationships (e.g., McFall-Ngai et al., 2013; Dishaw et al., 2014; Hammarlund 2020).

In addition to optimizing digestion, a large-scale chemical reactor requires reliable delivery of reactants. Although rangeomorphs preserve little direct evidence of their water processing habits, simply the turbulence generated by the elevated canopy and background currents will have ensured a continuous supply of food and gas exchange (Larsen & Riisgård,

1997; Lassen et al., 2006; Singer, Plotnik & Laflamme, 2012; Ghisalberti et al., 2014). By capitalizing on both the active hydrodynamics of their exposed mostly turbulent outsides, and unique chemical/microbial milieu of their contained and controlled 'insides,' chamber-forming rangeomorphs invented a fundamentally new way of feeding, breathing and making a living.

### **Rangeomorph affiliations**

A cnidarian grade of construction does not mean that rangeomorphs were necessarily cnidarians, but it usefully rules out a number of the usual suspects. There is, for example, no feasible means by which the cytoplasmic contents of coenocytic or syncytial eukaryotes could be replaced with sediment on time-scales compatible with the 3-D preservation of these soft-bodied organisms. Moreover, the absence of any known seaweeds using this sort of chambered, taphonomically castable construction makes an algal interpretation unlikely, even in photic-zone settings. Any convincing case for metazoan affiliation, however, requires the positive identification of diagnostically metazoan features, set in a phylogenetic context. Ignoring problematic ctenophores, there are currently three principal hypotheses for where rangeomorphs might reasonably be positioned within total-group Metazoa: 1) the sister-group of all extant animals (= stem-group Metazoa) (Xiao & Laflamme, 2009; Budd & Jensen, 2017; Dunn, Liu & Donoghue, 2017; Darroch et al., 2018); 2) the sister-group of all extant animals minus sponges (= stem-group Eumetazoa) (Buss & Seilacher, 1994; Dunn, Liu & Donoghue, 2017; Hoyal Cuthill & Han, 2018); and the sister-group of all extant cnidarians (= stem-group Cnidaria) (Dunn, Liu & Donoghue, 2017).

Despite the potential for confusing non-preservation with a true absence of derived characters (Sansom, Gabbott & Purnell, 2010), it is clear that rangeomorphs lacked a number of key crown-cnidarian attributes, not least an ability to move or respond usefully to

sedimentary inundation. Under comparable levels of event-bed sedimentation, modern actinarian and pennatulacean cnidarians engage in pronounced whole-organism/colony contraction – an escape response that both fluidizes surrounding sediments and precludes any infilling of gastrovascular compartments (Batham & Pantin, 1950; Kastendiek, 1976; Norris, 1989; Holst & Jarms, 2006; Chimienti, Angeletti & Mastrototaro, 2018). The conspicuously unresponsive habit of rangeomorphs reliably demonstrates their lack of cnidarian-grade muscle. It is also consistent with a lack of (muscle-activated) tentacles and a localized mouth, which in turn implies absence of a cnidarian-grade nerve net, predatory cnidae or predation-based feeding.

In the absence of muscle and associated systems, there appears to be little more to rangeomorphs than perforated bags of water charged by ciliary pumps. But even this represents a fundamental departure from protistan or sponge-grade, multicellularity (Arendt et al., 2015). At macroscopic length-scales, such a membranous structure can only be realistically achieved with the mechanical reinforcement afforded by specialized inter-cellular adhesion molecules and a collectivized, extracellular, basement membrane (Tyler, 2003; Nielsen, 2008; Jonusaite, Donini & Kelly, 2016). This type of differentiated epithelium is a uniquely eumetazoan feature – and its (inferred) identification in thin-walled rangeomorphs convincingly places these problematic fossils within total-group Eumetazoa (Budd & Jensen, 2017). The degree to which they can be more precisely resolved depends on the identification of additional phylogenetically informative characters. As pre-muscular, epithelial, tank-based digesters they offer a compelling model for stem-group eumetazoans. Insofar as macroscopically responsive muscle may have evolved independently in cnidarians and bilaterians (cf., Steinmetz et al., 2012), they might further be viewed as pre-muscular, pre-predatory, stem-group cnidarians (cf., Marcum & Campbell, 1978; Dunn, Liu & Donoghue, 2017).

There is much discussion over the nature of the ancestral (eu)metazoan, but the development of a gastrula phase – where the outside surface of a spherical blastula becomes sufficiently invaginated to act as an ‘inside’ – was undoubtedly a key innovation (Nielsen, 2008; Arendt et al., 2015). Although topologically equivalent to a solitary bag-like cnidarian, neither the gastrula nor its hypothetical ‘gastreae’ counterpart in early metazoan evolution is obviously comparable to macroscopic rangeomorphs, presumably because a large centralized mouth has no function in the absence of muscle, tentacles, or indeed any food particles large enough to require such an apparatus. In this context, there is a compelling argument for viewing these macroscopic fossils not as single organisms, but integrated suspension-feeding colonies, broadly analogous to those of extant pennatulacean and alcyonacean octocorals. Certainly the serially repeated pore-like structures in three-dimensionally preserved *Charnia* (Fig. 2) point to colony-like modularity (cf., Dewel, 2000; Dewel, Dewel & McKinney, 2001; Hoyal Cuthill & Conway Morris 2014; Dececchi et al., 2017; Kenchington, Dunn & Wilby, 2018), while the quantum increase in length-scales associated with coloniality would have provided fundamentally enhanced access to water-borne resources without the costs of developing a more sophisticated bodyplan (cf., Acuña, López-Urrutia & Colin, 2011; Pitt et al., 2013). Unlike predatory octocorals, however, all of the constituent individuals/modules of this hypothetical pre-muscular, colonial rangeomorph would have been deployed as cilia-powered, broadly gastreae-like ‘siphonozooids’ with a primary purpose in circulating water (Figs. 3c–d; 4). This does not mean that they are homologous with the siphonozooids of crown-group cnidarians, of course (cf., Landing et al., 2018). A colonial/modular suspension feeding habit is likely to have evolved independently in any number of stem-group metazoan lineages, just as it has among extant groups (Ryland & Warner, 1986).

## **Conclusion**

Rangeomorphs remain one of the most deeply problematic groups in the fossil record, even as ongoing work reveals novel developmental, anatomical and ecological detail (e.g., Sharp et al., 2017; Kenchington & Wilby, 2017; Dunn et al., 2018; Kenchington, Dunn & Wilby, 2018; Liu & Dunn, 2020). The present study yields yet further levels of biological resolution:

1. Rangeomorphs were not osmotrophic. The hydrodynamics associated with organisms of this size is physically and biochemically incompatible with such a habit.
2. Rangeomorphs were supported by a hydrostatic exoskeleton composed of seawater, as demonstrated by the ready castability of internalized chambers during event-bed sedimentation.
3. The rangeomorph body wall was thin-walled, comprising a biomechanically reinforced epithelium and associated mesoglea-like layer. This plastic, bag-like structure was breachable under high-energy siliciclastic sedimentation, but had sufficient integrity to allow three-dimensional casting in silt and sand.
4. Serially repeated lensoid structures developed (unilaterally) on at least some rangeomorph taxa potentially represent the openings through which seawater circulated in life. Smaller and/or non-preserved channels may also have fulfilled this role, analogous to the cryptic siphonozooids of some modern octocorals.
5. The flow of seawater through the rangeomorph chamber system is likely to have been driven by collective ciliary pumping, a plesiomorphic property of both metazoans and eukaryotes.
6. Rangeomorph chambers provided the controlled hydrodynamic and physiological circumstances necessary to conduct extracellular digestion and phagocytosis at macroscopic length-scales.

7. The constructional and functional anatomy of rangeomorphs identifies them as pre-muscular, total-group Eumetazoa.

Prior to the appearance of rangeomorphs there were just two feeding strategies available to free-living heterotrophic organisms: external digestion/osmotrophy as practiced by prokaryotes and fungi, and the more active capture and internal digestion of phagocytising protozoans (and sponges). Chamber-forming eumetazoans broke into this ancient duopoly, not by beating microbes at their own game, but through the invention of a revolutionary new technique for harvesting and processing food. By exploiting the unique potential of large size and compartmentalization, eumetazoans tapped into both the turbulent hydrodynamics of their 'outside' (discovering an effectively inexhaustible source of both food and gas exchange), and the controlled conditions of their 'inside' (allowing both extracellular digestion and 'osmotrophic' uptake to be conducted on an industrialized, CSTR-like scale). The key to all of this biological potential was a hydrostatic exoskeleton based on a bag-like epithelium charged by ciliary pumps. In one form or another such construction underpins the physiology of all eumetazoan life.

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Figure 1. Rangeomorph taxa illustrating the characteristic fractal-like branching and diversity of overall form. (a) *Charnia masoni*, type specimen, from Charnwood Forest, UK. (b) *Rangea schneiderhoehni*, type specimen, from Namibia. (c) *Hapsidophyllas flexibilis*, from SE Newfoundland. (d) *Fractofusus misrae* from SE Newfoundland. (e) *Bradgatia* sp. from SE Newfoundland. Scale bar: (a, e) = 2 cm; (b) = 1.5 cm; (c) = 4 cm; (d) = 3 cm. Photo credits: (a) Phil Wilby; (b) Dima Grazhdankin; (c) Olga Zhaxybayeva; (d) Alex Liu; (e) Jean-Bernard Caron.

Figure 2. Partially cast 3D specimens of *Charnia* from the Verkhovka Formation (Winter Mountains, White Sea, Russia), demonstrating the previous presence of water-filled chambers. (a, b) ‘upper’ and ‘lower’ surfaces of PIN 3993-7018 (with differential transfer of the primary branch casts between the two parts); note that only some parts of this specimen have been infilled with sediment (roughly the left-hand side of (a) and the right-hand side of (b)), with the remainder experiencing a more typical ‘collapse and death-mask’ type of preservation. The three serially repeated lensoid structures preserved on the upper side of the cast (arrows in (a)) potentially represent openings into the chambers; they are not present on the lower, fractally divided side (b), and are not preserved in collapsed parts of the frond. (c) cross-section through silt-cast primary branch of PIN 3993-7018, locally buried in mud and showing anatomical continuity between the chambers and serially repeated lensoid structures (arrowed); line of section indicated by dotted line in (b). (d) cross-section through silt-cast primary branch of PIN 3993-7018, locally buried in cross-laminated silt and showing erosive breaching/removal of the upper body wall; line of section indicated by asterisks in (b). (e) detail of a further silt-cast, mud-buried specimen (PIN 3992-7020) preserving serially repeated lensoid structures on the upper, non-fractally divided surface (arrows); the full

specimen is figured in Fedonkin (1994). Scale bar: (a, b, e) = 1 cm; (c) = 2.5 mm; (d) = 5 mm. PIN = Palaeontological Institute, Moscow. Photo credits: (a, b, c, e) Dima Grazhdankin; (d) Alex Liu.

Figure 3. Extant anthozoan cnidarians exhibiting features of relevance to the interpretation of Ediacaran rangeomorphs. (a) The modern actiniarian *Metridium*, demonstrating the disparate range of forms possible by a single specimen depending on the retention and deployment of seawater within the gastrovascular cavity. In the absence of muscle, such an organism would be unable to operate tentacles or a central mouth, though it could still (in principle) function as a suspension-feeding extra-cellular digestion chamber. (b) SEM of the colonial alcyonacean *Corallium* showing the surface expression of retracted autozooids (muscle-powered micro-predatory feeding polyps) and cryptically embedded siphonozooids (cilia-powered atentaculate polyps specialized for circulating seawater); the latter are unlikely to be recognizably preserved in the fossil record, even under the most exceptional taphonomic circumstances. (c) Schematic transverse section through a single siphonozooid of the colonial alcyonacean *Paragorgia* showing its ciliated water-pumping siphonoglyph (shaded in dark blue) and interconnecting gastrovascular canal system (light blue). (d) Schematic longitudinal section of *Paragorgia*, showing multiple water-pumping siphonozooids with cryptically small external openings (siphonoglyphs shaded in dark blue, gastrovascular canals light blue). Scale bar: (a) = 2 cm; (b, d) = 1 mm; (c) = 0.25 mm. (a) from Batham & Pantin (1950), reproduced with permission, *Journal of Experimental Biology*. (b) modified from Nonaka et al. (2012). (c, d) modified from Hickson (1883).

Figure 4. Schematic reconstruction of rangeomorph constructional/functional anatomy, and accompanying taphonomic pathways. (a) Chambered construction with a central mesoglea-

like layer (black) supporting a ciliated epithelium; external epidermis (brown) serves as an important locus of high *Re/Pe* gas exchange, whereas the internalized 'gastrodermis' (orange) offers anatomically created circumstances for feeding. Overall support is provided by transiently contained seawater. (b) Suspended DOC/POC is cycled through the internalized system via ciliary transport and siphonoglyph-like pumping. Chamber walls are likely to have hosted a diverse anaerobic microbiome (coloured dots), contributing to the gut-like extracellular digestion. (c) Three-dimensional casting of rangeomorph chambers following high-energy erosive breaching of the body-wall. (d) Collapse and two-dimensional 'death-mask' preservation where the body-wall remains intact, telescoping spatially separated features onto a single surface.