

Constructional and functional anatomy of Ediacaran rangeomorphs

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Original Article

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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 (high Re) and advective (high 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, most 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 body plan 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.

1. 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 period (c. 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 c. 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 macroscopic 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 organisms work in much the same way as their microscopic 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 (3D) 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 *et al.* 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 ($Re = UL/\nu$), and at elevated Péclet numbers where material exchange is dominated by advection rather than molecular diffusion ($Pe = UL/D$) (where ν is kinematic viscosity and D is 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 centimetre-scale branching element that exhibits self-similarity over three or four ‘fractal’ levels (Narbonne, 2004; Brasier *et al.* 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*),

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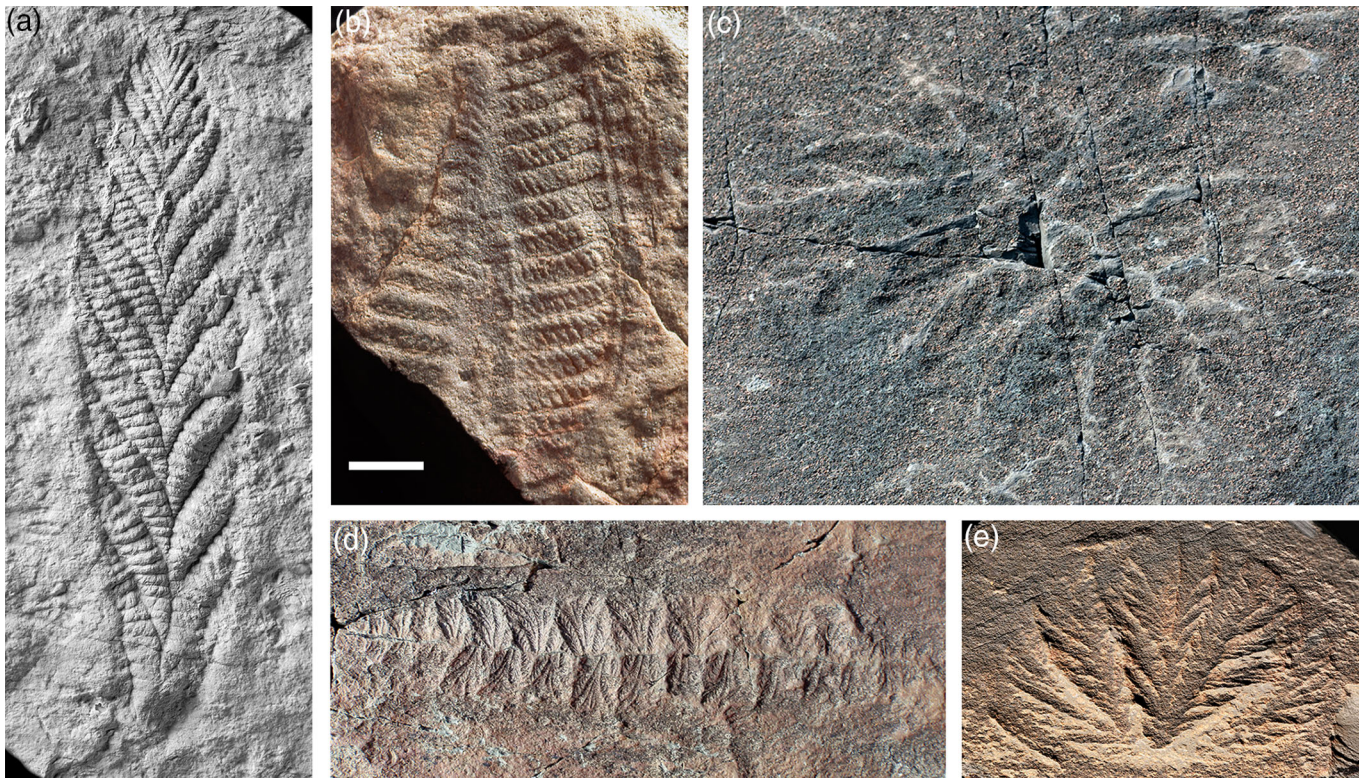


Fig. 1. (Colour online) Rangeomorph taxa illustrating the characteristic fractal-like branching and diversity of overall form. (a) *Charnia masoni*, type specimen, from Charnwood Forest, UK. (b) *Rangea schneiderhoehni*, type specimen, from Namibia. (c) *Hapsidophyllas flexibilis*, from SE Newfoundland.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

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 *et al.* 2009; Sperling *et al.* 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 *et al.* 2015).

1.a. Osmotrophy and dissolved organic carbon: 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 *et al.* 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 *et al.* 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 and 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 μm (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 one-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 (from *c.* 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 leading to long-term 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 *et al.* 1992; Sutherland *et al.* 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 *et al.* 2005; Skikne *et al.* 2009; Gori *et al.* 2014; Blewett & Goss, 2017). There are also reports of uncharacterized DOC uptake (e.g. Roditi *et al.* 2000; Barnard *et al.* 2006; Rengefors *et al.* 2008), although 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 those associated with internalized 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 & Perenthaler, 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 *et al.* 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 *et al.* 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 *et al.* 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.

2. 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 where neither substrate digestion nor advective loss are relevant factors (*Sporospirillum praeclarum* in tadpoles and *Epulopiscium fishelsoni* in surgeon fish). None of the remaining five taxa is osmotrophic, or even heterotrophic: *Thiomargarita*, *Achromatium*, *Beggiatoa* and *Thiovulum* are all sulphur-oxidizing chemoautotrophs, and *Prochloron* is a cyanobacterial photoautotroph. Indeed, the most likely explanation for the exceptionally large dimensions of these primary producers is the advective delivery of (freely diffusible) CO_2 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 (cf. Schulz & Jørgensen, 2001; Laflamme *et al.* 2009, fig. 4b).

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 *et al.* 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 gut-dwelling *Sporospirillum* and *Epulopiscium* (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 follow-up incorporation (enhanced at low *Re*) is to separate the two processes. At a unicellular level, the contained intracellular digestion of POC and DOC by phagocytizing protists by-passes many of the fluid-dynamic challenges faced by osmotrophic prokaryotes, although new ones inevitably arise, not least the elevated *Re* and turbulence associated with larger eukaryotic cells, and their interference with effective prey capture (Dolan *et al.* 2003). At macroscopic length scales, phagocytosis becomes entirely untenable without anatomical or behavioural adaptations for attenuating flow, as seen in the ramifying aquiferous system of sponges (Leys & Eerkes-Medrano, 2006), the enveloping habit of placozoans (Smith *et al.* 2015) or 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, although these notably constitute just a fraction of the total surface area.

What the macroscopic size of rangeomorphs certainly does confer is elevated Reynolds and Péclet 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 macrobenthos 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 O₂ and CO₂; indeed, all three of the datasets used by Ghisalberti *et al.* (2014, figs 3, 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 *et al.* 2012). Additional ventilatory effects are likely to have been generated by a ciliated epithelium, 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).

2.a. 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, 1992; Seilacher *et al.* 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 2D 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 3D 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 3D profile (Fedonkin, 1994; Grazhdankin, 2004; Dunn *et al.* 2018), even as adjacent unfilled areas collapsed to yield a more typical 2D 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 2D 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, 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 of 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; Nonaka *et al.* 2012; Williams *et al.* 2012), and it is notable that the millimetre-sized siphonozooids of certain pennatulaceans fail to preserve even under the most optimized laboratory burial conditions (Norris, 1989).

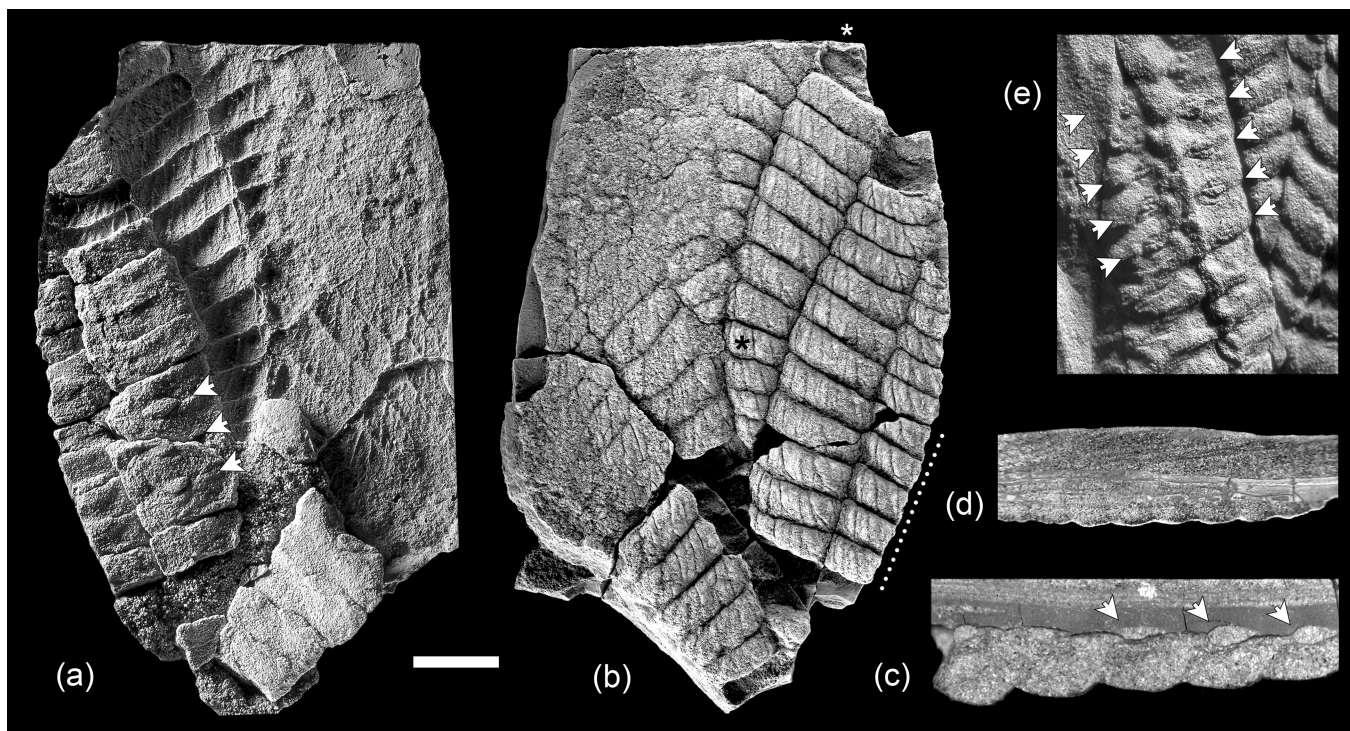


Fig. 2. Partially cast 3D specimens of *Charnia* from the Verkhovka Formation (Winter Mountains, White Sea, Russia), demonstrating the previous presence of water-filled chambers. (a, b) 'Upper' and 'lower' surfaces of PIN 3993-7018 (with differential transfer of the primary branch casts between the two 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 a 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 the dotted line in (b). (d) Cross-section through a silt-cast primary branch of PIN 3993-7018, locally buried in cross-laminated silt and showing clear evidence of erosive breaching and loss 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; and (d) 5 mm. PIN – Palaeontological Institute, Moscow. Photo credits: (a, b, c, e) Dima Grazhdankin; and (d) Alex Liu.

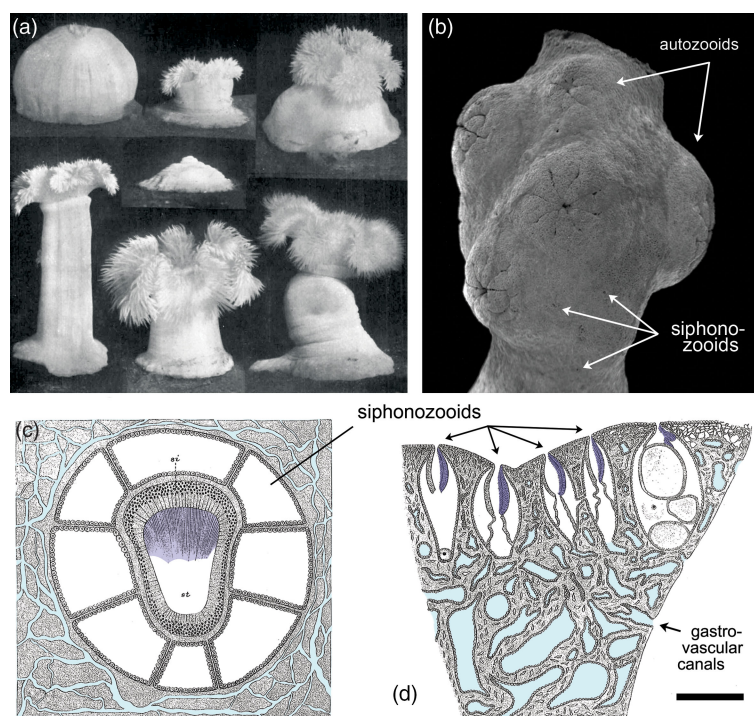


Fig. 3. (Colour online) Extant anthozoan cnidarians exhibiting features of relevance to the interpretation of Ediacaran rangemorphs. (a) The modern actinarian *Metridium*, demonstrating the disparate range of forms possible by a single specimen depending on the retention and deployment of seawater within the gastrovascular cavity. In the absence of muscle, such an organism would be unable to operate tentacles or a central mouth, although it could still (in principle) function as a suspension-feeding extra-cellular digestion chamber. (b) Scanning electron micrograph (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 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 dark blue, gastrovascular canals light blue). Scale bar: (a) 2 cm; (b, d) 1 mm; and (c) 0.25 mm. (a) From Batham & Pantin (1950), reproduced with permission of the *Journal of Experimental Biology*. (b) Modified from Nonaka et al. (2012). (c, d) Modified from Hickson (1883).

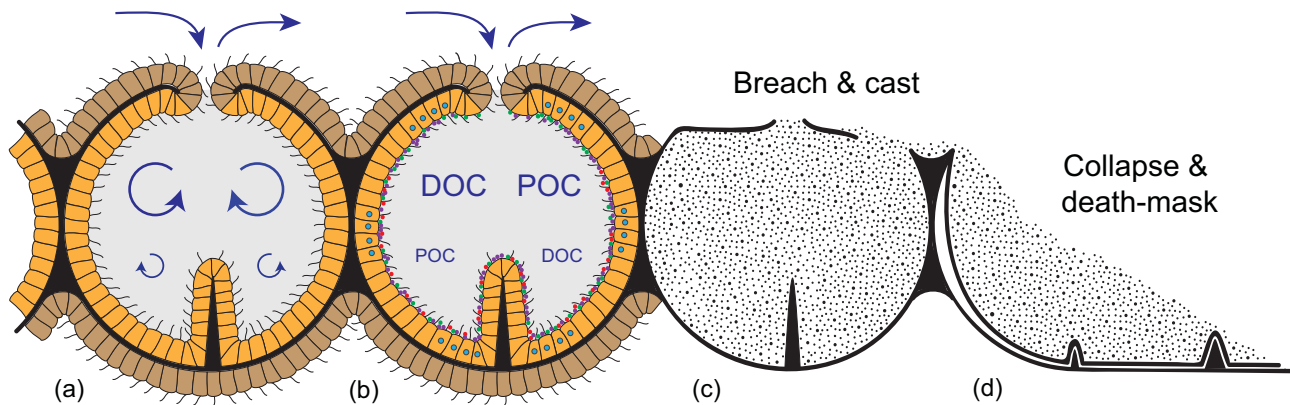


Fig. 4. (Colour online) Schematic reconstruction of the constructional and functional anatomy of rangeomorphs, alongside possible taphonomic pathways. (a) Chambered construction with a central mesoglea-like layer (black) supporting a ciliated epithelium; external epidermis (brown) serves as an important locus of high Re/Pe gas exchange, whereas the internalized 'gastrodermis' (orange) is optimized for feeding at macroscopic length scales. Overall support is provided by transiently contained seawater (grey). (b) Suspended DOC and POC is cycled through the internalized system via ciliary transport and siphonoglyph-like pumping. Chamber walls are likely to have hosted a diverse, mostly anaerobic microbiome (coloured dots), contributing to gut-like extracellular digestion. (c) Three-dimensional casting of rangeomorph chambers following high-energy erosive breaching of the body wall. (d) Collapse and 2D 'death-mask' preservation where the body wall remains intact; the telescoping of spatially separated features onto a single surface yields specimens that appear similar on both surfaces, and obscures key aspects of the original anatomy.

Considering that 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 upwards-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 millimetre-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* also appear not to define external morphology, but rather internalized mesentery-like structures – presumably 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 in living organisms are almost universally guarded by ciliated and/or contractile cells. Full 3D 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 route of silt-entraining currents would have been through abrasive breaches in the thin body wall (cf. de Bettignies *et al.* 2012). Indeed, the depositional

continuity from fossil-casting silts to overlying cross-laminated horizons in PIN 3993-7018 (Fig. 2d) demonstrates the localized erosion of upwards-facing portions of the frond; it is only where the casts are locally succeeded 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 and/or 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 *et al.* 2018; Dunn *et al.* 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 3D casts through to essentially 2D 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 point to a similar grade of chambered construction and hydrostatic support.

2.b. 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, that is, within a bag-like hydrostatic (exo)skeleton. There is nothing particularly exotic about such a system; indeed, it is the primary means of structural support among basal eumetazoans. In actiniarian (sea anemones) and pennatulacean (sea pens, etc.) anthozoans, for example, it is transiently retained seawater in the gastrovascular system that provides the antagonist against which epithelial muscle acts to generate overall 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, typically expressed in the form of channelized siphonoglyphs (Fig. 3c, d). This self-supporting bag-like construction offers an exceptionally parsimonious means of assembling a macroscopic organism, not based on costly biominerals, differentiated tissue systems or co-lemic 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 *et al.* 2011) and an enveloping epithelial layer to ensure its integrity (Fig. 4a) (cf. Tyler, 2003; Jonusaite *et al.* 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 *et al.* 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 middle Ediacaran deposits. 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 and interconnection of water-pumping siphonozooids and stolon systems (Fig. 3c, d) (Hickson, 1883; Brafield, 1969; Williams *et al.* 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 'fractally' partitioned hydrostatic exoskeleton of rangeomorphs was 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 *et al.* 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 actiniarian and pennatulacean anthozoans, rhythmic cycling between hypoxic and anoxic conditions within the gastrovascular system (Brafield & Chapman, 1967; Chapman, 1972; Jones *et al.* 1977; Brafield, 1980) reflects the active suppression of oxygen levels, even in the presence of regularly transiting oxygenated seawater (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 to 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 *et al.* 2012; Ghisalberti *et al.* 2014). By capitalizing on both the active hydrodynamics of their exposed mostly turbulent outsides, and the unique chemical and microbial milieu of their semi-contained 'insides', chamber-forming rangeomorphs invented a fundamentally new way of feeding, breathing and making a living.

2.c. 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 timescales compatible with the 3D 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 *et al.* 2017; Darroch *et al.* 2018); (2) the sister-group of all extant animals minus sponges (stem-group Eumetazoa) (Buss & Seilacher, 1994; Dunn *et al.* 2017; Hoyal Cuthill & Han, 2018); or (3) the sister-group of all extant cnidarians (stem-group Cnidaria) (Dunn *et al.* 2017).

Despite the potential for confusing non-preservation with a true absence of derived characters (Sansom *et al.* 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 or whole-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 *et al.* 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 intercellular adhesion molecules and a collectivized, extracellular, basement membrane (Tyler, 2003; Nielsen, 2008; Jonusaite *et al.* 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. To the extent that macroscopically responsive striated muscle appears to 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 *et al.* 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 ‘gastraea’ 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 as integrated suspension-feeding colonies, broadly analogous to those of extant pennatulacean and alcyonacean octocorals. The serially repeated pore-like structures in three-dimensionally preserved *Charnia* (Fig. 2) certainly point to colony-like modularity (cf. Dewel, 2000; Dewel *et al.* 2001; Hoyal Cuthill & Conway Morris, 2014; Decocchi *et al.* 2017; Kenchington *et al.* 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 body plan (cf. Acuña *et al.* 2011; Pitt *et al.* 2013). Unlike predatory octocorals, however, all of the constituent individuals or modules of this hypothetical pre-muscular, colonial rangeomorph would have been deployed as cilia-powered, broadly gastraea-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 or 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).

3. 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 *et al.* 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 are 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 integument 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 lenoid 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 pleiomorphic 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 plus osmotrophy as practiced by prokaryotes and fungi, and the more active capture and internal digestion of phagocytizing 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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References

- Acuña JL, López-Urrutia Á and Colin S (2011) Faking giants: the evolution of high prey clearance rates in jellyfishes. *Science* **333**, 1627–9.
- Agostini S, Suzuki Y, Higuchi T, Casareto BE, Yoshinaga K, Nakano Y and Fujimura H (2012) Biological and chemical characteristics of the coral gastric cavity. *Coral Reefs* **31**, 147–56.
- Antcliffe JB and Brasier MD (2007) *Charnia* and sea pens are poles apart. *Journal of the Geological Society* **164**, 49–51.
- Arendt D, Benito-Gutierrez E, Brunet T and Marlow H (2015) Gastric pouches and the mucociliary sole: setting the stage for nervous system evolution. *Philosophical Transactions of the Royal Society B* **370**, 20150286.
- Arnosti C (2011) Microbial extracellular enzymes and the marine carbon cycle. *Annual Review of Marine Science* **3**, 401–25.
- Arrieta JM, Mayol E, Hansman RL, Herndl GJ, Dittmar T and Duarte CM (2015) Dilution limits dissolved organic carbon utilization in the deep ocean. *Science* **348**, 331–3.
- Baines SB, Fisher NS and Cole JJ (2005) Uptake of dissolved organic matter (DOM) and its importance to metabolic requirements of the zebra mussel, *Dreissena polymorpha*. *Limnology and Oceanography* **50**, 36–47.
- Barnard C, Martineau C, Frenette J-J, Dodson JJ and Vincent WF (2006) Trophic position of zebra mussel veligers and their use of dissolved organic carbon. *Limnology and Oceanography* **51**, 1473–84.
- Batham EJ and Pantin CFA (1950) Muscular and hydrostatic action in the sea-anemone *Metridium senile* (L.). *Journal of Experimental Biology* **27**, 264–89.
- Batham EJ and Pantin CFA (1951) The organization of the muscular system of *Metridium senile*. *Journal of Cell Science* **92**, 27–54.
- Blewett TA and Goss GG (2017) A novel pathway of nutrient absorption in crustaceans: branchial amino acid uptake in the green shore crab (*Carcinus maenas*). *Proceedings of the Royal Society B* **284**, 20171298.
- Brafield AE (1969) Water movements in the pennatulid coelenterate *Pteroides griseum*. *Journal of Zoology* **158**, 317–25.
- Brafield AE (1980) Oxygen consumption by the sea anemone *Calliactis Parasitica* (Couch). *Journal of Experimental Biology* **88**, 367–74.
- Brafield AE and Chapman G (1967) The respiration of *Pteroides griseum* (Bohadsch) a pennatulid coelenterate. *Journal of Experimental Biology* **46**, 97–104.
- Brasier MD, Antcliffe JB and Liu AG (2012) The architecture of Ediacaran fronds. *Palaeontology* **55**, 1105–24.
- Brasier MD, Liu AG, Menon L, Matthews JJ, McIlroy D and Wacey D (2013) Explaining the exceptional preservation of Ediacaran rangeomorphs from Spaniard's Bay, Newfoundland: a hydraulic model. *Precambrian Research* **231**, 122–35.
- Budd GE and Jensen S (2017) The origin of the animals and a 'Savannah' hypothesis for early bilaterian evolution. *Biological Reviews* **92**, 446–73.
- Buss LW and Seilacher A (1994) The phylum Vendobionta: a sister group of the Eumetazoa? *Paleobiology* **20**, 1–4.
- Butterfield NJ (2003) Exceptional fossil preservation and the Cambrian explosion. *Integrative and Comparative Biology* **43**, 166–77.
- Butterfield NJ (2018) Oxygen, animals and aquatic bioturbation: an updated account. *Geobiology* **16**, 3–16.
- Camilleri JC and Ribí G (1986) Leaching of dissolved organic carbon (DOC) from dead leaves, formation of flakes from DOC, and feeding on flakes by crustaceans in mangroves. *Marine Biology* **91**, 337–44.
- Catling DC, Glein CR, Zahnle KJ and McKay CP (2005) Why O₂ is required by complex life on habitable planets and the concept of planetary 'oxygenation time'. *Astrobiology* **5**, 415–38.
- Cavalier-Smith T (2017) Origin of animal multicellularity: precursors, causes, consequences—the choanoflagellate/sponge transition, neurogenesis and the Cambrian explosion. *Philosophical Transactions of the Royal Society B* **372**, 20150476.
- Chapman G (1958) The hydrostatic skeleton in the invertebrates. *Biological Reviews* **33**, 338–71.
- Chapman G (1972) A note on the oxygen consumption of *Renilla köllikeri*, Pfeffer. *Comparative Biochemistry and Physiology Part A* **42**, 63–866.
- Chimienti G, Angeletti L and Mastrototaro F (2018) Withdrawal behaviour of the red sea pen *Pennatula rubra* (Cnidaria: Pennatulacea). *The European Zoological Journal* **85**, 64–70.
- Confer DR and Logan BE (1991) Increased bacterial uptake of macromolecular substrates with fluid shear. *Applied and Environmental Microbiology* **57**, 3093–100.
- Darroch SAF, Smith EF, Laflamme M and Erwin DH (2018) Ediacaran extinction and Cambrian explosion. *Trends in Ecology & Evolution* **33**, 653–63.
- de Bettignies T, Thomsen MS and Wernberg T (2012) Wounded kelps: patterns and susceptibility to breakage. *Aquatic Botany* **17**, 223–33.
- Decocchi TA, Narbonne GM, Greentree C and Laflamme M (2017) Relating Ediacaran fronds. *Paleobiology* **43**, 171–80.
- de Goeij JM, van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, de Goeij AFPM and Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* **342**, 108–10.
- DeLong JP, Okie JG, Moses ME, Sibly RM and Brown JH (2010) Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. *Proceedings of the National Academy of Sciences* **107**, 12941–5.
- Dewel RA (2000) Colonial origin for Eumetazoa: major morphological transitions and the origin of bilaterian complexity. *Journal of Morphology* **243**, 35–74.
- Dewel RA, Dewel WC and McKinney FK (2001) Diversification of the Metazoa: Ediacarans, colonies, and the origin of eumetazoan complexity by nested modularity. *Historical Biology* **15**, 193–218.
- Dishaw LJ, Cannon JP, Litman GW and Parker W (2014) Immune-directed support of rich microbial communities in the gut has ancient roots. *Developmental & Comparative Immunology* **47**, 36–51.
- Dolan JR, Sall N, Metcalfe A and Gasser B (2003) Effects of turbulence on the feeding and growth of a marine oligotrich ciliate. *Aquatic Microbial Ecology* **31**, 183–92.
- Droser ML, Tarhan LG, Evans SD, Surprenant RL and Gehling JG (2020) Biostratigraphy of the Ediacara Member (Rawnsley Quartzite, South Australia): implications for depositional environments, ecology and biology of Ediacara organisms. *Interface Focus* **10**, 20190100.
- Duckworth AR (2003) Effect of wound size on the growth and regeneration of two temperate subtidal sponges. *Journal of Experimental Marine Biology and Ecology* **287**, 139–53.

- Dufour SC and McIlroy D** (2017) Ediacaran pre-placozoan diploblasts in the Avalonian biota: the role of chemosynthesis in the evolution of early animal life. In *Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier* (eds AT Brasier, D McIlroy and N McLoughlin), pp. 211–9. Geological Society of London, Special Publication no. 448.
- Dunn FS, Liu AG and Donoghue PCJ** (2017) Ediacaran developmental biology. *Biological Reviews* **93**, 914–32.
- Dunn FS, Liu AG and Gehling JG** (2019) Anatomical and ontogenetic reassessment of the Ediacaran frond *Arborea arborea* and its placement within total group Eumetazoa. *Palaeontology* **62**, 851–65.
- Dunn FS, Wilby PR, Kenchington CG, Grazhdankin DV, Donoghue PCJ and Liu AG** (2018) Anatomy of the Ediacaran rangeomorph *Charnia masoni*. *Papers in Palaeontology* **5**, 157–76.
- Dzik J** (2002) Possible ctenophoran affinities of the Precambrian “sea-pen” *Rangaea*. *Journal of Morphology* **252**, 315–34.
- Eckert EM and Perenthaler J** (2014) Bacterial epibionts of *Daphnia*: a potential route for the transfer of dissolved organic carbon in freshwater food webs. *The ISME Journal* **8**, 1808–19.
- Fedonkin MA** (1994) Vendian body fossils and trace fossils. In *Early Life on Earth (Nobel Symposium No. 84)* (ed. S Bengtson), pp. 370–88. New York: Columbia University Press.
- Fedonkin MA and Ivantsov AY** (2007) *Ventogyrus*, a possible siphonophore-like trilobozoan coelenterate from the Vendian sequence (late Neoproterozoic), northern Russia. In *The Rise and Fall of the Ediacaran Biota* (eds P Vickers-Rich and P Komarower), pp. 187–94. Geological Society of London, Special Publication no. 286.
- Flood PR, Deibel D and Morris CC** (1992) Filtration of colloidal melanin from sea water by planktonic tunicates. *Nature* **355**, 630–2.
- Follett CL, Repeta DJ, Rothman DH, Xu L and Santinelli C** (2014) Hidden cycle of dissolved organic carbon in the deep ocean. *Proceedings of the National Academy of Sciences* **111**, 16706–11.
- Ford TD** (1958) Pre-Cambrian fossils from Charnwood Forest. *Proceedings of the Yorkshire Geological Society* **31**, 211–7.
- Friedman ES, Bittinger K, Esipova TV, Hou L, Chau L, Jiang J, Mesaros C, Lund PJ, Liang X, FitzGerald GA, Goulian M, Lee D, Garcia BA, Blair IA, Vinogradov SA and Wu GD** (2018) Microbes vs. chemistry in the origin of the anaerobic gut lumen. *Proceedings of the National Academy of Sciences* **115**, 4170–5.
- Ghisalberti M, Gold DA, Laflamme M, Clapham ME, Narbonne GM, Summons RE, Johnston DT and Jacobs DK** (2014) Canopy flow analysis reveals the advantage of size in the oldest communities of multicellular eukaryotes. *Current Biology* **24**, 305–309.
- Glazier DS** (2006) The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience* **56**, 325–32.
- Goldberg WM** (2018) Coral food, feeding, nutrition, and secretion: a review. In *Marine Organisms as Model Systems in Biology and Medicine* (eds M Kloc and JZ Kubiak), pp. 377–421. Cham, Switzerland: Springer.
- Gori A, Grover R, Orejas C, Sikorski S and Ferrier-Pagès C** (2014) Uptake of dissolved free amino acids by four cold-water coral species from the Mediterranean Sea. *Deep Sea Research Part II* **99**, 42–50.
- Grazhdankin D** (2004) Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology* **30**, 203–21.
- Grazhdankin D** (2014) Patterns of evolution of the Ediacaran soft-bodied biota. *Journal of Paleontology* **88**, 269–83.
- Grazhdankin D and Seilacher A** (2005) A re-examination of the Nama-type Vendian organism *Rangaea schneiderhoehni*. *Geological Magazine* **142**, 571–82.
- Guizien K and Ghisalberti M** (2016) Living in the canopy of the animal forest: physical and biogeochemical aspects. In *Marine Animal Forests* (eds S Rossi, L Bramanti, A Gori and C Orejas Saco del Valle), pp. 1–22. Cham, Switzerland: Springer International Publishing.
- Hammarlund EU** (2020) Harnessing hypoxia as an evolutionary driver of complex multicellularity. *Interface Focus* **10**, 20190101.
- Hansell DA** (2013) Recalcitrant dissolved organic carbon fractions. *Annual Review of Marine Science* **5**, 421–445.
- Harmata KL, Parrin AP, Morrison PR, McConnell KK, Bross LS and Blackstone NW** (2013) Quantitative measures of gastrovascular flow in octocorals and hydroids: toward a comparative biology of transport systems in cnidarians. *Invertebrate Biology* **132**, 291–304.
- Hickson SJ** (1883) On the ciliated groove (siphonoglyphe) in the stomodaeum of the alcyonarians. *Philosophical Transactions of the Royal Society of London* **174**, 693–705.
- Holley MC and Shelton GAB** (1984) Reversal of the direction of mucus-flow on the ciliated pharynx of a sea anemone. *Journal of Experimental Biology* **108**, 151–61.
- Holst S and Jarms G** (2006) Responses of solitary and colonial coronate polyps (Cnidaria, Scyphozoa, Coronatae) to sedimentation and burial. *Journal of Experimental Marine Biology and Ecology* **329**, 230–8.
- Höss S, Bergtold M, Haitzer M, Traunspurger W and Steinberg CEW** (2001) Refractory dissolved organic matter can influence the reproduction of *Caenorhabditis elegans* (Nematoda). *Freshwater Biology* **46**, 1–10.
- Hoyal Cuthill JF and Conway Morris S** (2014) Fractal branching organizations of Ediacaran rangeomorph fronds reveal a lost Proterozoic body plan. *Proceedings of the National Academy of Sciences* **111**, 13122–6.
- Hoyal Cuthill JF and Han J** (2018) Cambrian petalonamid *Stromatoveris* phylogenetically links Ediacaran biota to later animals. *Palaeontology* **61**, 813–23.
- Hurd CL** (2000) Water motion, marine macroalgal physiology, and production. *Journal of Phycology* **36**, 453–72.
- Ivantsov AY** (2016) Reconstruction of *Charniodiscus yorgensis* (macrobiota from the Vendian of the White Sea). *Paleontological Journal* **50**, 1–12.
- Ivantsov AY and Grazhdankin DV** (1997) A new representative of the Petalonamae from the Upper Vendian of the Arkhangelsk region. *Paleontological Journal* **31**, 1–16.
- Jenkins RJ** (1985) The enigmatic Ediacaran (late Precambrian) genus *Rangaea* and related forms. *Paleobiology* **11**, 336–55.
- Jenkins RJF and Nedin C** (2007) The provenance and palaeobiology of a new multi-vened, chambered frondose organism from the Ediacaran (later Neoproterozoic) of South Australia. In *The Rise and Fall of the Ediacaran Biota* (eds P Vickers-Rich and P Komarower), pp. 195–222. Geological Society of London, Special Publication no. 286.
- Jones WC, Pickthall VJ and Nesbitt SP** (1977) A respiratory rhythm in sea anemones. *Journal of Experimental Biology* **68**, 187–198.
- Jonusaite S, Donini A and Kelly SP** (2016) Occluding junctions of invertebrate epithelia. *Journal of Comparative Physiology B* **186**, 17–43.
- Jumars PA, Deming JW, Hill PS, Karp-Boss L, Yager PL and Dade WB** (1993) Physical constraints on marine osmotrophy in an optimal foraging context. *Aquatic Microbial Ecology* **7**, 121–59.
- Kahn AS, Yahel G, Chu JWF, Tunnicliffe V and Leys SP** (2015) Benthic grazing and carbon sequestration by deep-water glass sponge reefs. *Limnology and Oceanography* **60**, 78–88.
- Kamran Z, Zellner K, Kyriazis H, Kraus CM, Reynier J-B and Malamy JE** (2017) In vivo imaging of epithelial wound healing in the cnidarian *Clytia hemisphaerica* demonstrates early evolution of purse string and cell crawling closure mechanisms. *BMC Developmental Biology* **17**, 17.
- Karp-Boss L, Boss E and Jumars PA** (1996) Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. *Oceanography and Marine Biology* **34**, 71–108.
- Kastendiek J** (1976) Behavior of the sea pansy *Renilla kollikeri* Pfeffer (Coelenterata: Pennatulacea) and its influence on the distribution and biological interactions of the species. *The Biological Bulletin* **151**, 518–37.
- Kenchington CG, Dunn FS and Wilby PR** (2018) Modularity and overcompensatory growth in Ediacaran rangeomorphs demonstrate early adaptations for coping with environmental pressures. *Current Biology* **28**, 3330–6.
- Kenchington CG and Wilby PR** (2017) Rangeomorph classification schemes and intra-specific variation: are all characters created equal? In *Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier* (eds AT Brasier, D McIlroy and N McLoughlin), pp. 211–50. Geological Society of London, Special Publication no. 448.
- Koehl MAR** (1996) When does morphology matter? *Annual Review of Ecology and Systematics* **27**, 501–42.
- Laflamme M, Gehling JG and Droser ML** (2018) Deconstructing an Ediacaran frond: three-dimensional preservation of *Arborea* from Ediacara, South Australia. *Journal of Paleontology* **92**(3), 323–35.

- Laflamme M, Xiao S and Kowalewski M** (2009) Osmotrophy in modular Ediacara organisms. *Proceedings of the National Academy of Sciences* **106**, 14438–43.
- Landing E, Antcliffe JB, Geyer G, Kouchinsky A, Bowser SS and Andreas A** (2018) Early evolution of colonial animals (Ediacaran Evolutionary Radiation–Cambrian Evolutionary Radiation–Great Ordovician Biodiversification interval) *Earth-Science Reviews* **178**, 105–35.
- Langlois V, Andersen A, Bohr T, Visser A, Fishwick J and Kiorbøe T** (2009) Significance of swimming and feeding currents for nutrient uptake in osmotrophic and interception feeding flagellates. *Aquatic Microbial Ecology* **54**, 35–44.
- Larsen PS and Riisgård HU** (1997) Biomixing generated by benthic filter feeders: a diffusion model for near-bottom phytoplankton depletion. *Journal of Sea Research* **37**, 81–90.
- Lassen J, Kortegrd M, Riisgård HU, Friedrichs M, Graf G and Larsen PS** (2006) Down-mixing of phytoplankton above filter-feeding mussels—interplay between water flow and biomixing. *Marine Ecology Progress Series* **314**, 77–88.
- Leys SP and Eerkes-Medrano DI** (2006) Feeding in a calcareous sponge: particle uptake by pseudopodia. *The Biological Bulletin* **211**, 157–71.
- Litvak Y, Byndloss MX and Bäuml AJ** (2018) Colonocyte metabolism shapes the gut microbiota. *Science* **362**, eaat9076.
- Liu AG and Dunn FS** (2020) Filamentous connections between Ediacaran fronds. *Current Biology* **30**, 1322–8.
- Liu AG, Kenchington CG and Mitchell EG** (2015) Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota. *Gondwana Research* **27**, 1355–80.
- Maeda H, Kumagai T, Matsuoka H and Yamazaki Y** (2010) Taphonomy of large *Canadoceras* (ammonoid) shells in the Upper Cretaceous Series in South Sakhalin, Russia. *Paleontological Research* **14**, 56–68.
- Marcum BA and Campbell RD** (1978) Development of *Hydra* lacking nerve and interstitial cells. *Journal of Cell Science* **29**, 17–33.
- Mari X, Passow U, Migon C, Burd AB and Legendre L** (2017) Transparent exopolymer particles: effects on carbon cycling in the ocean. *Progress in Oceanography* **151**, 13–37.
- McFall-Ngai M, Hadfield MG, Bosch TCG, Carey HV, Domazet-Lošo T, Douglas AE, Dubilier N, Eberl G, Fukami T, Gilbert SF, Hentschel U, King N, Kjelleberg S, Knoll AH, Kremer N, Mazmanian SK, Metcalf JL, Nealon K, Pierce NE, Rawls JF, Reid A, Ruby EG, Rumpho M, Sanders JG, Tautz D and Wernegreen JJ** (2013) Animals in a bacterial world, a new imperative for the life sciences. *Proceedings of the National Academy of Sciences* **110**, 3229–36.
- Mcmeans BC, Koussoroplis A-M, Arts MT and Kainz MJ** (2015) Terrestrial dissolved organic matter supports growth and reproduction of *Daphnia magna* when algae are limiting. *Journal of Plankton Research* **37**, 1201–09.
- McMenamin M** (1993) Osmotrophy in fossil protocists and early animals. *Invertebrate Reproduction & Development* **23**, 165–6.
- Menzel D** (1988) How do giant plant cells cope with injury?—The wound response in siphonous green algae. *Protoplasma* **144**, 73–91.
- Moran MA, Kujawinski EB, Stubbins A, Fatland R, Aluwihare LI, Buchan A, Crump BC, Dorrestein PC, Dyhrman ST, Hess NJ, Howe B, Longnecker K, Medeiros PM, Niggemann J, Obernosterer I, Repeta DJ and Waldbauer JR** (2016) Deciphering ocean carbon in a changing world. *Proceedings of the National Academy of Sciences* **113**, 3143–51.
- Narbonne GM** (2004) Modular construction of early Ediacaran complex life forms. *Science* **305**, 1141–44.
- Nielsen C** (2008) Six major steps in animal evolution: are we derived sponge larvae? *Evolution & Development* **10**, 241–57.
- Nonaka M, Nakamura M, Tsukahara M and Reimer JD** (2012) Histological examination of precious corals from the Ryukyu Archipelago. *Journal of Marine Biology* **2012**, 1–14.
- Norris RD** (1989) Cnidarian taphonomy and affinities of the Ediacara biota. *Lethaia* **22**, 381–93.
- Parrin AP, Netherton SE, Bross LS, McFadden CS and Blackstone NW** (2010) Circulation of fluids in the gastrovascular system of a stoloniferan octocoral. *Biological Bulletin* **219**, 112–21.
- Penry DL and Jumars PA** (1986) Chemical reactor analysis and optimal digestion. *BioScience* **36**, 310–15.
- Penry DL and Jumars PA** (1987) Modeling animal guts as chemical reactors. *The American Naturalist* **129**, 69–96.
- Pitt KA, Duarte CM, Lucas CH, Sutherland KR, Condon RH, Mianzan H, Purcell JE, Robinson KL and Uye S-I** (2013) Jellyfish body plans provide allometric advantages beyond low carbon content. *PLoS ONE* **8**, e72683.
- Plante CJ** (1990) Digestive associations between marine detritivores and bacteria. *Annual Review of Ecology and Systematics* **21**, 93–127.
- Pollak PE and Montgomery WL** (1994) Giant bacterium (*Epulopiscium fishelsoni*) influences digestive enzyme activity of an herbivorous surgeonfish (*Acanthurus nigrofuscus*). *Comparative Biochemistry and Physiology Part A* **108**, 657–62.
- Raz-Bahat M, Douek J, Moiseeva E, Peters EC and Rinkevich B** (2017) The digestive system of the stony coral *Stylophora pistillata*. *Cell and Tissue Research* **368**, 311–23.
- Rengfors K, Pålsson C, Hansson L and Heiberg L** (2008) Cell lysis of competitors and osmotrophy enhance growth of the bloom-forming alga *Gonyostomum semen*. *Aquatic Microbial Ecology* **51**, 87–96.
- Retallack GJ** (1994) Were the Ediacaran fossils lichens? *Paleobiology* **20**, 523–44.
- Rex G** (1985) A laboratory flume investigation of the formation of fossil stem fills. *Sedimentology* **32**, 245–55.
- Richards TA and Talbot NJ** (2013) Horizontal gene transfer in osmotrophs: playing with public goods. *Nature Reviews Microbiology* **11**, 720–7.
- Roditi HA, Fisher NS and Sanudo-Wilhelmy SA** (2000) Uptake of dissolved organic carbon and trace elements by zebra mussels. *Nature* **407**, 78–80.
- Runnegar B** (1982) Oxygen requirements, biology and phylogenetic significance of the late Precambrian worm *Dickinsonia*, and the evolution of the burrowing habit. *Alcheringa* **6**, 223–39.
- Ryland JS and Warner GF** (1986) Growth and form in modular animals: ideas on the size and arrangement of zooids. *Philosophical Transactions of the Royal Society of London B* **313**, 53–76.
- Sansom RS, Gabbott SE and Purnell MA** (2010) Non-random decay of chor-date characters causes bias in fossil interpretation. *Nature* **463**, 797–800.
- Schick MJ** (1991) *A Functional Biology of Sea Anemones*. London: Chapman & Hall, 395 pp.
- Schlesinger A, Zlotkin E, Kramarsky-Winter E and Loya Y** (2009) Cnidarian internal stinging mechanism. *Proceedings of the Royal Society of London B* **276**, 1063–7.
- Schlüchter D** (1991) A perforated gastrovascular cavity in the symbiotic deep-water coral *Leptoseris fragilis*: a new strategy to optimize heterotrophic nutrition. *Helgolander Meeresuntersuchungen* **45**, 423–43.
- Schulz HN and Jørgensen BB** (2001) Big bacteria. *Annual Reviews in Microbiology* **55**, 105–37.
- Sebens KP** (1987) The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics* **18**, 371–407.
- Seilacher A** (1970) Preservational history of ceratite shells. *Palaentology* **14**, 16–21.
- Seilacher A** (1989) Vendozoa: organismic construction in the Proterozoic biosphere. *Lethaia* **22**, 229–39.
- Seilacher A** (1992) Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Journal of the Geological Society* **149**, 607–13.
- Seilacher A, Grazhdankin D and Legouta A** (2003) Ediacaran biota: the dawn of animal life in the shadow of giant protists. *Paleontological Research* **7**, 43–54.
- Shapiro OH, Fernandez VI, Garren M, Guasto JS, Debailon-Vesque FP, Kramarsky-Winter E, Vardi A and Stocker R** (2014) Vortical ciliary flows actively enhance mass transport in reef corals. *Proceedings of the National Academy of Sciences* **111**, 13391–6.
- Sharp AC, Evans AR, Wilson SA and Vickers-Rich P** (2017) First non-destructive internal imaging of *Rangea*, an icon of complex Ediacaran life. *Precambrian Research* **299**, 303–08.
- Sharp JH** (1973) Size classes of organic carbon in seawater. *Limnology and Oceanography* **18**, 441–7.
- Sher D, Fishman Y, Melamed-Book N, Zhang M and Zlotkin E** (2008) Osmotically driven prey disintegration in the gastrovascular cavity of the green hydra by a pore-forming protein. *FASEB Journal* **22**, 207–14.
- Shields GA** (2017) Earth system transition during the Tonian–Cambrian interval of biological innovation: nutrients, climate, oxygen and the marine organic carbon capacitor. In *Earth System Evolution and Early Life: A*

- Celebration of the Work of Martin Brasier* (eds AT Brasier, D McIlroy and N McLoughlin), pp. 167–77. Geological Society of London, Special Publication no. 448.
- Short MB, Solari CA, Ganguly S, Powers TR, Kessler JO and Goldstein RE** (2006) Flows driven by flagella of multicellular organisms enhance long-range molecular transport. *Proceedings of the National Academy of Sciences* **103**, 8315–9.
- Singer A, Plotnik R, and Laflamme M** (2012) Experimental fluid dynamics of an Ediacaran frond. *Palaeontologia Electronica* **15**, 1–14.
- Skikne SA, Sherlock RE and Robison BH** (2009) Uptake of dissolved organic matter by ephyrae of two species of scyphomedusae. *Journal of Plankton Research* **31**, 1563–70.
- Smith CL, Pivovarova N and Reese TS** (2015) Coordinated feeding behavior in *Trichoplax*, an animal without synapses. *PLoS ONE* **10**, e0136098.
- Smith HL and Waltman PE** (1995) *The Theory of the Chemostat: Dynamics of Microbial Competition*. Cambridge: Cambridge University Press, 332 pp.
- Solari CA, Kessler JO and Goldstein RE** (2007) Motility, mixing, and multicellularity. *Genetic Programming and Evolvable Machines* **8**, 115–29.
- Southward AJ** (1955) Observations on the ciliary currents of the jelly-fish *Aurelia aurita* L. *Journal of the Marine Biological Association of the United Kingdom* **34**, 201–16.
- Sperling EA, Peterson KJ and Laflamme M** (2011) Rangeomorphs, *Thectardis* (Porifera?) and dissolved organic carbon in the Ediacaran oceans. *Geobiology* **9**, 24–33.
- Steinmetz PRH** (2019) A non-bilaterian perspective on the development and evolution of animal digestive systems. *Cell and Tissue Research* **377**, 321–39.
- Steinmetz PRH, Kraus JEM, Larroux C, Hammel JU, Amon-Hassenzahl A, Houlston E, Wörheide G, Nickel M, Degnan BM and Technau U** (2012) Independent evolution of striated muscles in cnidarians and bilaterians. *Nature* **487**, 231–4.
- Sutherland KR, Madin LP and Stocker R** (2010) Filtration of submicrometer particles by pelagic tunicates. *Proceedings of the National Academy of Sciences* **107**, 15129–34.
- Thingstad TF, Øvreås L, Egge JK, Løvdal T and Haldal M** (2005) Use of non-limiting substrates to increase size; a generic strategy to simultaneously optimize uptake and minimize predation in pelagic osmotrophs? *Ecology Letters* **8**, 675–82.
- Tucker RP, Shibata B and Blankenship TN** (2011) Ultrastructure of the mesoglea of the sea anemone *Nematostella vectensis* (Edwardsiidae). *Invertebrate Biology* **130**, 11–24.
- Tyler S** (2003) Epithelium—the primary building block for metazoan complexity. *Integrative and Comparative Biology* **43**, 55–63.
- Verdugo P, Alldredge AL, Azam F, Kirchman DL, Passow U and Santschi PH** (2004) The oceanic gel phase: a bridge in the DOM–POM continuum. *Marine Chemistry* **92**, 67–85.
- Vetter YA, Deming JW, Jumars PA and Krieger-Brockett BB** (1998) A predictive model of bacterial foraging by means of freely released extracellular enzymes. *Microbial Ecology* **36**, 75–92.
- Vickers-Rich P, Yu Ivantsov A, Trusler PW, Narbonne GM, Hall M, Wilson SA, Greentree C, Fedonkin MA, Elliott DA, Hoffmann KH and Schneider GIC** (2013) Reconstructing *Rangaea*: new discoveries from the Ediacaran of southern Namibia. *Journal of Paleontology* **87**, 1–15.
- Viver T, Orellana LH, Hatt JK, Urdiain M, Díaz S, Richter M, Antón J, Avian M, Amann R, Konstantinidis KT and Rosselló-Móra R** (2017) The low diverse gastric microbiome of the jellyfish *Cotylorhiza tuberculata* is dominated by four novel taxa. *Environmental Microbiology* **19**, 3039–58.
- Williams GC, Hoeksema BW and Van Ofwegen LP** (2012) A fifth morphological polyp in pennatulacean octocorals, with a review of polyp polymorphism in the genera *Pennatula* and *Pteroeides* (Anthozoa: Pennatulidae). *Zoological Studies* **51**, 1006–17.
- Wood DA, Dalrymple RW, Narbonne GM, Gehling JG and Clapham ME** (2003) Paleoenvironmental analysis of the late Neoproterozoic Mistaken Point and Trepassey formations, southeastern Newfoundland. *Canadian Journal of Earth Sciences* **40**, 1375–91.
- Wright SH and Manahan DT** (1989) Integumental nutrient uptake by aquatic organisms. *Annual Review of Physiology* **51**, 585–600.
- Xiao S and Laflamme M** (2009) On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends in Ecology & Evolution* **24**, 31–40.
- Yahel G, Sharp JH, Marie D, Häse C and Genin A** (2003) In situ feeding and element removal in the symbiont-bearing sponge *Theonella swinhoei*: bulk DOC is the major source for carbon. *Limnology and Oceanography* **48**, 141–9.