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Constructional and functional anatomy of Ediacaran rangeomorphs

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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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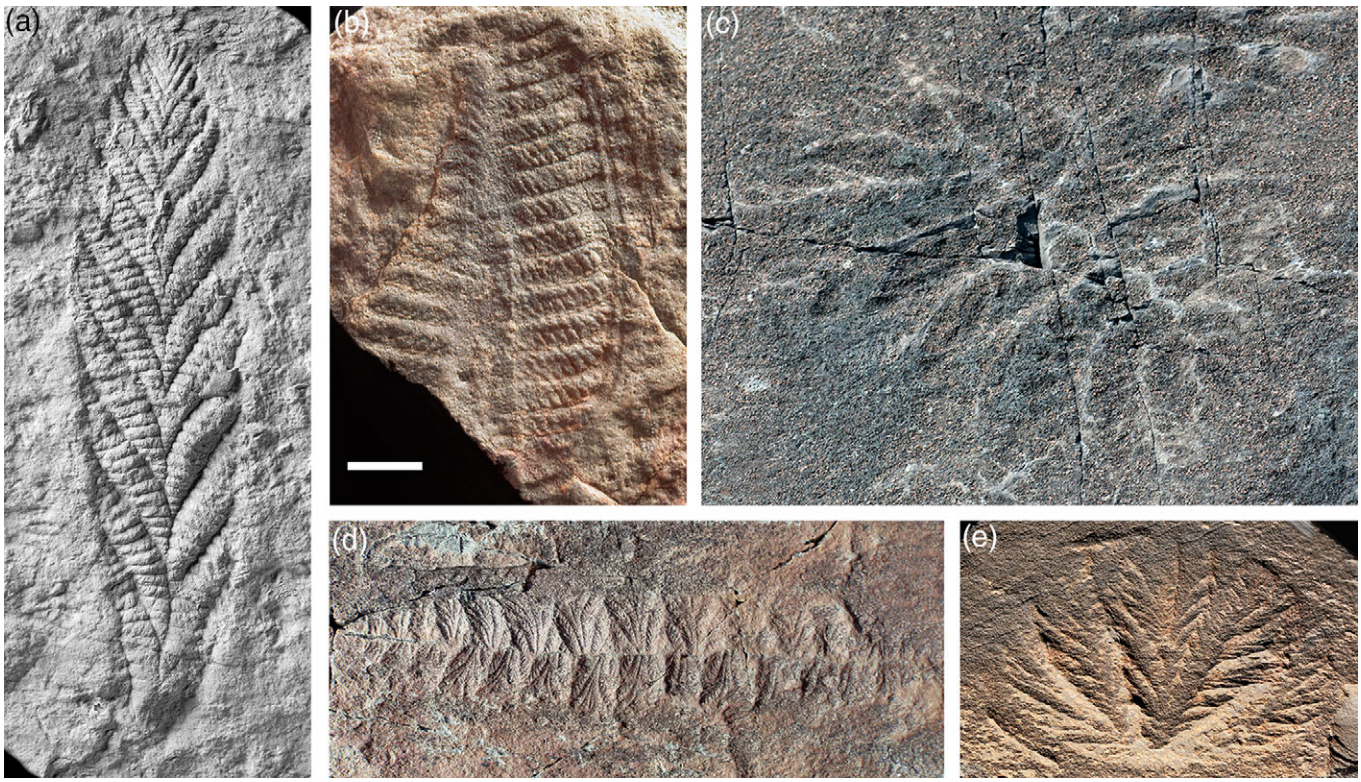


Fig. 1. Rangeomorph taxa illustrating the characteristic fractal-like branching and diversity of overall form. (a) *Charnia masoni*, type specimen, from Charnwood Forest, UK. (b) *Rangea schneiderhoehni*, type specimen, from Namibia. (c) *Hapsidophyllas flexibilis*, from SE Newfoundland. (d) *Fractofusus 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 ($<< Re$). 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

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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 μmol 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 & Ribi, 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 & Ribi, 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 *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

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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 O_2 and CO_2; 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).

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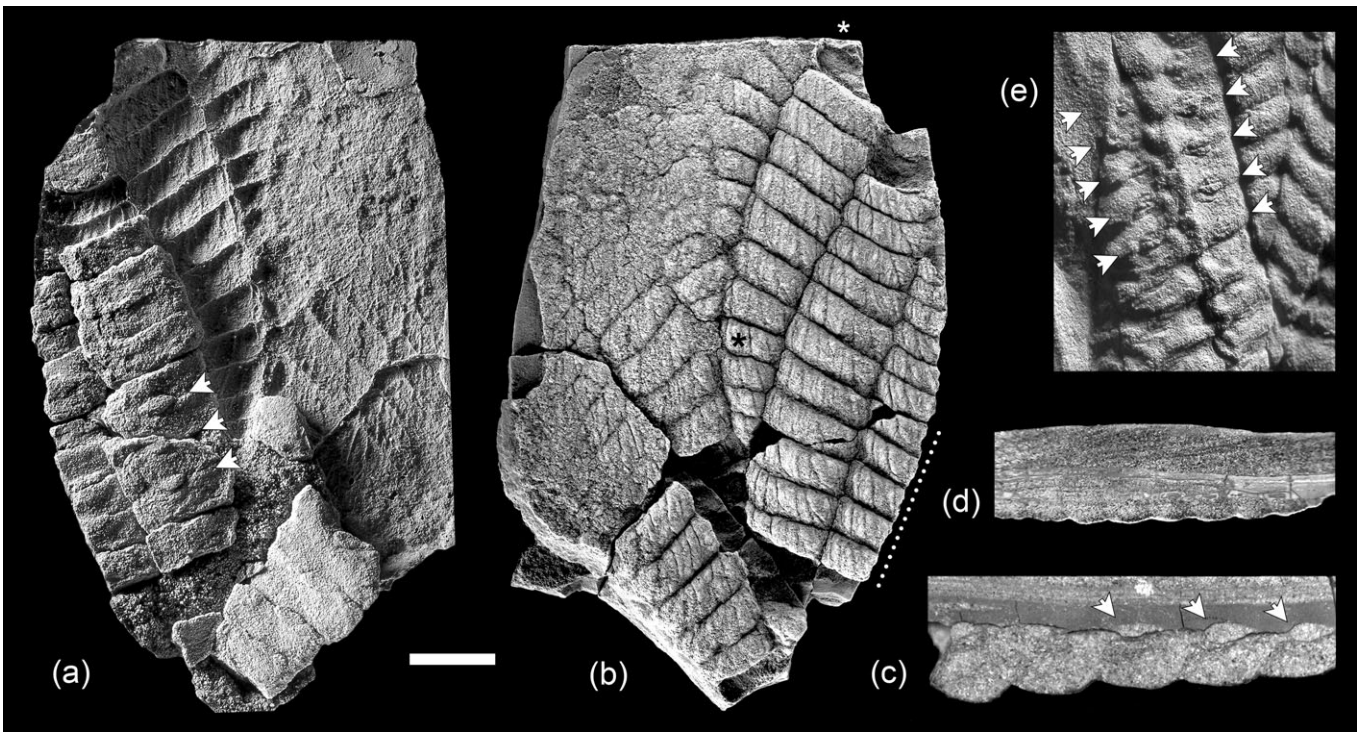


Fig. 2. Partially cast 3D specimens of *Charnia* from the Verkhovka Formation (Winter Mountains, White Sea, Russia), demonstrating the previous presence of water-filled chambers. (a, b) 'Upper' and 'lower' surfaces of PIN 3993-7018 (with differential transfer of the primary branch casts between the two 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.

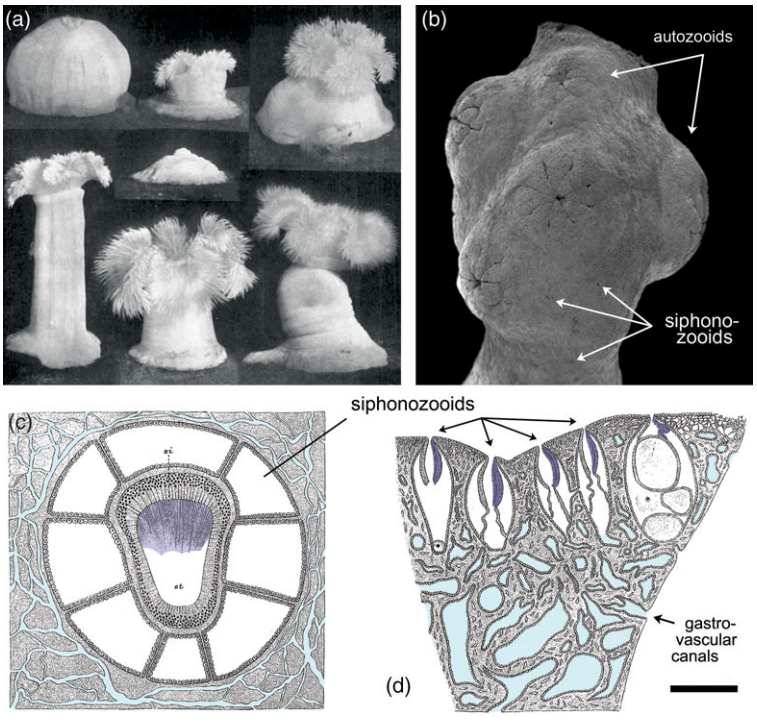


Fig. 3. Extant anthozoan cnidarians exhibiting features of relevance to the interpretation of Ediacaran rangeomorphs. (a) The modern actiniarian *Metridium*, demonstrating the disparate range of forms possible by a single specimen depending on the retention and deployment of seawater within the gastrovascular cavity. In the absence of muscle, such an organism would be unable to operate tentacles or a central mouth, 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).

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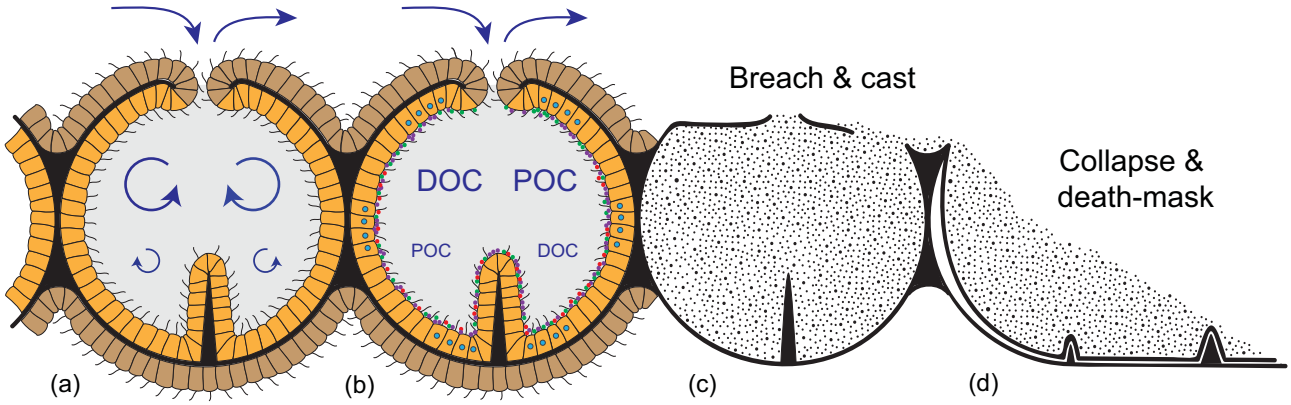


Fig. 4. Schematic reconstruction of the constructional and functional anatomy of rangeomorphs, alongside possible taphonomic pathways. (a) Chambered construction with a central mesoglea-like layer (black) supporting a ciliated epithelium; external epidermis (brown) serves as an important locus of high *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 *Rangea* 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.

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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 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 *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 (Schlicter, 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.

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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 actiniarian 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; Dececchi *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 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

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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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