Ediacaran pre-placozoan diploblasts in the Avalonian biota: the role of chemosynthesis in the evolution of early animal life

SUZANNE C. DUFOUR¹ & DUNCAN MCILROY²*

¹Department of Biology, Memorial University of Newfoundland, St John’s, NL, Canada A1B 3X9
²Department of Earth Sciences, Memorial University of Newfoundland, St John’s, NL, Canada A1B 3X5

*Correspondence: dmcilroy@mun.ca

Abstract: The large, enigmatic members of the Ediacaran biota have received much attention regarding their possible affinities and mode of life. Fossil evidence reveals that many Ediacaran animals, such as the rangeomorphs, were characterized by extensive surface areas, lived in close association with the seafloor and were non-motile. We argue for the presence of a simple, diploblastic body plan in these early animals and discuss the means by which they probably derived nutrients from chemosynthetic bacteria thriving at the sediment–water interface. We consider that the large surface area of some Ediacaran organisms in the Avalonian biota may have been an adaptation for maximizing a phagocytotic or chemosymbiotic surface. Ediacaran animals probably increased the availability of oxygen along their ventral surface either by diffusion or ciliary pumping. This increased supply of oxygen to the sediment is inferred to have simultaneously increased the productivity of their food source (chemosynthetic bacteria) and restricted the build-up of toxic sulphides in the pore waters below their bodies. This is an example of a very simple form of ecosystem engineering.

Some of the earliest known Ediacaran macrofossils have been found in c. 580 myr-old, deep, sub-photic zone marine deposits in southeastern Newfoundland and form the so-called Avalonian biota (Narbonne 2005); other early macrofossils, such as those from the Lantian biota, are of uncertain age (Budd & Jensen 2015). The majority of the Avalonian macro-biota is represented by non-mineralized epibenthic macro-organisms, which, even in the oldest fossiliferous strata, grew to up to 1 m in length or 20 cm in diameter (Narbonne & Gehling 2003; Liu et al. 2011, 2016; Fig. 1a, b). One of the characteristics of this fossil assemblage is that the organisms were almost exclusively sessile, with only rare surficial metazoan trails in strata c. 565 myr old and younger (Liu et al. 2010) until the first phase of ichnological radiation in the latest Ediacaran at c. 550 Ma (Jensen 2003). It would therefore seem that for almost 30 myr prior to 550 Ma, the seafloor of Avalonia was dominated by large Ediacaran macro-organisms that were sessile and either (1) epibenthic, reclining on the sediment surface (e.g. Fractofusus; Fig. 1c) or tethered to it by a discoidal surficial holdfast (e.g. Charniodiscus Laflamme et al. 2004; Fig. 1d) or (2) hemibenthic, having a bulbous holdfast within the sediment (e.g. Trepassia Brasier et al. 2013; Fig. 1a, e).

The biological affinity of Ediacaran organisms remains enigmatic, but recent work tends to characterize them as stem- or crown-group metazoans (see Liu et al. 2014, 2015), potentially representing multiple clades that have been preserved under a common taphonomic regime (Xiao & Laflamme 2009). Molecular clock data suggest that the origin of metazoans predates the late Ediacaran period, with many major clades radiating during the Cryogenian and early Ediacaran (dos Reis et al. 2015; Erwin 2015). There is no convincing direct evidence for triploblastic features and complex internal organs among the Ediacaran macrofossils and a simple diploblastic bauplan consisting of multiple modules along a polarized body axis is typically invoked for these organisms (Laflamme et al. 2009; Budd & Jensen 2015), with the possible exception of the latest Ediacaran mollusc-like Kimberella (e.g. Ivantsov 2009; Vinther 2015). We propose that some elements of the soft-bodied Ediacara biota possessed a simple architecture consisting of an epithelial surface enclosing mesenchyme (i.e. inert, predominantly acellular material), similar to the body plan of extant placozoa, as has been proposed for the mollic late Ediacaran organism Dickinsonia (Sperling & Vinther 2010). An important difference between the placozoan model for...
Dickinsonia and the characteristics of the earliest Ediacaran biotas, as described in this paper, is the immobility of the latter, which constrains their possible modes of feeding. Extant placozoans lack a digestive system and therefore cannot support ingestive feeding modes. Instead, cells from the lower epithelium secrete exoenzymes that lyse surficial microalgae in mat grounds and the resultant breakdown products of extracellular digestion are absorbed by ventral cells (i.e. the ‘digestive sole’) for nutrition (Smith et al. 2014, 2015a). Once the matground food resource has been exploited, the placozoan must move away to find additional food, but also to avoid the build-up of sulphide in the pore waters beneath it (Loenarz et al. 2011; cf. McIlroy et al. 2009). Feeding using a placozoan-like ventral digestive sole has been proposed as a stage in metazoan evolution that predates the evolution of a gut (Arendt et al. 2015). Motile placozoans such as Trichoplax use ciliary gliding and amoeboid movement following the local digestion of microbial mats, as is invoked for the Ediacaran organisms Yorgia and Dickinsonia (Ivantsov & Malakovskaya 2002; Dzik 2003; Fedonkin 2003; Gehling et al. 2005; Seilacher 2007; Sperling & Vinther 2010).

Fig. 1. The earliest Ediacaran macrofossils from (a, b) the Drook Formation, (c, d) the Mistaken Point Formation and (e) the Trepassey Formation of southeastern Newfoundland. (a) Trepasia wardae, a large frondose Ediacaran organism (scale bar 5 cm). (b) Large ivesheadiomorph fossils up to 20 cm in diameter considered to represent decayed remnants of the Ediacaran biota (scale bar 4 cm). (c) Fractofusus misrai showing fractal-like rangeomorph-type branching (scale bar 4 cm). (d) Charniodiscus showing the basal holdfast, stem and frond that could have been periodically held into the water column for oxygen collection (scale bar 4 cm). (e) Holdfast of a frondose Ediacaran showing that the holdfasts of some taxa were anchored within the sediment (scale bar 4 cm).
on the basis of *Epibain* trace fossils (Ivantsov 2013). However, immobile Ediacaran forms must have used a different feeding strategy that required no motility.

**Feeding strategies of Ediacaran organisms**

Most previous interpretations of the feeding strategies of sessile Ediacarans focused on either suspension feeding/filter feeding (the uptake of particulate organic matter) or osmotrophy, i.e. the uptake of dissolved organic matter (DOM). These interpretations are founded in the large-scale morphological similarities between frondose Ediacarans and sea pens. The former have been broadly considered to be suspension feeders (e.g. Clapham et al. 2003), but this has been shown to be inaccurate (Antcliffe & Brasier 2007); more recent computational models support passive suspension feeding in the enigmatic *Tribrachidium* (Rahman et al. 2015). However, clear evidence for the presence of pores allowing the uptake of particulate matter is currently lacking (Liu et al. 2015). Alternatively, DOM could be absorbed through cell surfaces, as has been proposed for Ediacaran forms with large surface areas such as rangeomorphs (Laflamme et al. 2009). Although DOM uptake may be theoretically feasible in Ediacaran organisms if the metabolically active layers are fairly thin (Laflamme et al. 2009), it remains questionable whether the size and quality of the DOM reservoir were sufficient to sustain such large organisms using osmotrophy alone (Johnston et al. 2012; Liu et al. 2015).

It has been proposed that Ediacaran organisms could also have relied on symbionts as a source of nutrients, a hypothesis that has largely been rejected because photosymbiosis could not be supported in the deep-water marine setting of the Avalonian Ediacaran biota given the low availability of light. Chemosymbiosis has also occasionally been considered as a possible feeding mode for Ediacaran organisms (Seilacher 1984; McMenamin & McMenamin 1990; McMenamin 1998; Liu et al. 2015), but has been dismissed partly on the grounds that the inferred tiering of the Avalonian biota is similar to modern suspension feeding communities and does not show the patchiness expected of (presumably vent-related) chemosynthetic communities (Laflamme & Narbonne 2008).

**Chemosynthetic feeding modes in Ediacaran organisms**

In the absence of significant surficial bioturbation prior to about 550 Ma (Jensen 2003), a redoxcline would have developed at the sediment–water interface due to microbial sulphate reduction of the sedimentary biomass from matgrounds and pelagic fallout (McIlroy & Logan 1999). Sulphide pore waters at the seafloor pose significant metabolic challenges to immotile epifaunal and hemibenthic organisms such as the early Ediacaran biota due to the toxicity of pore water sulphides. Common microbial inhabitants of redoxclines include chemolithoautotrophs, such as the sulphur-oxidizing bacteria that derive energy for carbon fixation from the oxidation of reduced sulphur (e.g. Howarth 1984). The likely abundance of sulphate-reducing bacteria close to the seafloor means that the immotile Ediacaran organisms must have developed adaptations to reduce the impact of sulphide on the ventral epithelium. Considering that oxygen was available, at least periodically, in the overlying water (Hood & Wallace 2014; Wood et al. 2015; Cui et al. 2016; Sahoo et al. 2016), the upper surface of Ediacaran organisms is likely to have been adapted for oxygen uptake. Oxygen transport could have occurred within a diploblastic Ediacaran animal by diffusion through the mesoglea, which could also have stored oxygen during periods of hypoxia, as demonstrated in the mesoglea of modern scyphomedusae (Thuesen et al. 2005; Pitt et al. 2013). Alternatively, in frondose or plicate taxa, ciliary pumping could lead to the transport of oxygenated water to the ventral surface (Fig. 2). The net effect of diffusion and/or the ciliary transport of oxygen to the ventral surface of Ediacaran organisms would be to enhance the productivity of chemolithoautotrophs in the pore water system near the organism (McIlroy & Logan 1999). It would also oxidize the sulphides in pore waters and thereby avoid tissue damage. We consider it likely that this closely integrated microbe–macrobiotic biogeochemical interaction created a food resource for the Ediacaran macrobiota and may have fuelled their large size. The derivation of nutrition from the sedimentary microbiota by immotile Ediacaran organisms, such as the rangeomorphs, could have been achieved in a number of different ways using some combination of phagotrophy and chemosymbiosis.

**Phagotrophy**

Immotile Ediacaran macro-organisms such as the sediment-reclining form *Fractofusus* (Fig. 1c) could have efficiently acquired nutrients from chemolithoautotrophic microbes through non-ingestive processes, including the use of the high surface area ventral epithelium as a phagocytic surface (Fig. 2). Phagotrophy, the uptake and subsequent digestion of larger particles such as microbes and particulate matter, is a fundamental property of eukaryotes (Fenchel 2012). Supporting evidence for such a mode of life in certain rangeomorphs is provided by the field observation that *Fractofusus* commonly...
Fig. 2. Diagrammatic reconstruction of the quilted fractal-like branching of the immotile Ediacaran taxon Fractofusus showing details of the means by which the organism might have interacted with the underlying substrate. The lower diagram shows the oxygenation of the lower surface using waves of ciliary contraction and diffusion. The supply of oxygen is likely to have stimulated microbial productivity in the adjacent sediment. The top row shows different possible modes of feeding for the immotile Ediacaran organisms. Green circles represent the distribution and abundance of chemolithoautotrophs and the curved arrows show the diffusion of solutes. From left to right the modes of feeding depicted are: phagotrophy, with irrigation using cilia; ectosymbiosis; endosymbiosis; and endosymbiosis in a trophosome, which would require a thin organism and the diffusion of sulphide/methane throughout the organism. POM, particulate organic matter.
grow on ivesheadiomorphs (Fig. 3), which are considered to represent local concentrations of necromass (Liu et al. 2011). Such hotspots of microbial productivity were created by the decomposition of earlier generations of Ediacarans that lived on the same surface (Liu et al. 2011). Ivesheadiomorphs might therefore be considered as the Ediacaran analogue of modern whale falls that are loci of chemosynthesis on the modern seafloor (Krogh 1934; Budd & Jensen 2015; Smith et al. 2015). We note that few other taxa in the Mistaken Point biota grew on top of other Ediacaran organisms and that Fractofusus was not readily transported (Gehling & Narbonne 2007), so the association is unlikely to be accidental.

Animals that feed by phagotrophy, such as the Porifera, may attain large sizes even in the absence of a digestive tract provided that they have a large internal surface area (e.g. canals lined with choanoocytes) for feeding. In contrast with the Porifera, many sessile Ediacaran forms such as Fractofusus and Charniodiscus (Fig. 1c, d) have a large external surface area that could also be involved in microbial phagocytosis. Epithelial surfaces involved in chemosynthetic phagotrophy require fewer cell types than a placozoan-like mucociliary sole that releases exoenzymes. Animals at the gastraeal or pre-gastraeal grade of organization have four cell types: mucocytes, glandular cells for digestive enzyme production, ciliary cells, and cells specialized in nutrient uptake (Arendt et al. 2015). The placozoan Trichoplax secretes mucus to: (1) facilitate ciliary locomotion; (2) provide a substrate for micro-algal digestion; and (3) allow the cilia of the ventral surface to produce both co-ordinated motility and the churning action that facilitates ingestion (Smith et al. 2015a). The epithelium of chemosynthetic phagotrophs, in contrast, requires a less complex grade of organization because no glandular cell is required for exoenzyme production. Epithelial surfaces of immotile Ediacaran chemosynthetic phagotrophs could, at their simplest, consist of cells with an apical microvillar layer, specialized in nutrient uptake. Chemosynthetic phagotrophy could therefore be considered to be an evolutionary precursor to the placozoan grade of organization, characterized by a digestive ventral epithelium (Arendt et al. 2015) that requires, in its most simple form, mucociliary motility to find new food resources.

Chemosymbiosis

A wide variety of extant macroinvertebrates living at the interface between oxic and anoxic environments gain nutrients from chemosynthetic sulphur-oxidizing and/or methanotrophic bacteria (Duperron et al. 2005; Dubilier et al. 2008). Although some animals graze on these microbes, an ingestive process that is comparatively metabolically expensive, others have evolved symbioses with chemolithoautotrophs in which the host typically provides oxygen to, and directly obtains nutrients from, populations of bacteria (Dubilier et al. 2008). Extant macro-organisms with chemosymbiotic feeding strategies (e.g. thiotrophy and methanotrophy) are anatomically more complex and include organs and tissue types that cannot be confidently inferred from the majority of even the best-preserved Ediacaran organisms (Brasier & Antcliffe 2008). It is possible, however, that organisms with much simpler, gutless body plans could also be chemosymbiotic.

Most known chemosymbiotic animals maintain their symbionts within cells (Dubilier et al. 2008). Others, such as thyasirid and some bathymodiolid bivalves, establish extracellular symbioses with thiotrophic and/or methanotrophic chemolithoautotrophic bacteria that they phagocytose for intracellular digestion (Dufour 2005; Duperron et al. 2005). Extracellular symbioses are generally considered to be simpler than endocellular symbioses (Smith 1979; Rosati 2004), but both types could have existed among the immotile elements of the Ediacaran biota (Fig. 2). Endocellular symbionts could be maintained in either (1) the ventral epithelial cells of Ediacaran organisms such as Fractofusus that lie on the seafloor (Fig. 2) or (2) in an internal mass of cells analogous to the trophosome of the mouthless flatworm Paracatenula, which has been described as
the most primitive chemosymbiotic animal known (Gruber-Vodicka et al. 2011; Fig. 2). Ectosymbionts associated with Ediacaran organisms could either have been associated with the ventral surface of reclining forms that were constantly in contact with the seafloor (Fig. 2), or possibly with the surface of fronds that were episodically held in contact with the seafloor (see Fig. 4).

The fractal-like growth patterns of permanently sessile reclining Ediacaran organisms such as Fractofusus (Seilacher 1992; Gehling & Narbonne 2007) that maximize the ventral surface area of the organism are considered here to be adaptations for chemosynthetic feeding or symbiosis (Fig. 1c, 2). Otherwise, the growth of extensive surfaces in direct contact with reducing pore waters makes no logical sense. Chemosynthetic feeding modes require no gut and are energetically efficient because there is no production of exoenzymes as required by the mucociliary digestive sole of a placozoan grade organism (Sperling & Vinther 2010; Arendt et al. 2015). A phagotrophic or chemosymbiotic organism does not need to compete with smaller eukaryotes or prokaryotes for the products of extracellular digestion. Intracellular symbiosis, in particular, is highly ecologically efficient and can support the growth and metabolism of large gutless organisms living at the redoxcline; however, the maintenance of high growth rates in large chemosymbiotic animals such as the vent tubeworm Riftia pachyptila requires adaptations for supplying oxygen to symbionts (Childress & Girguis 2011). Mesoglea-rich dolioloblastic organisms have both a low oxygen demand and a low carbon content (Pitt et al. 2013), which facilitates the growth of large organisms with a high surface area to volume ratio, such as characterizes the Ediacara biota. Very large surface areas enable high rates of metabolite and waste product diffusion and are the most important characteristic of the symbiont-bearing organs of extant chemosymbiotic animals (e.g. bivalve gills; Childress & Girguis 2011). Chemosymbiosis or chemosynthetic phagotrophy could thereby explain the hitherto unresolved conundrum of why the first fossil organisms were so large (Narbonne 2011).

The giant epibenthic ectosymbiotic colonial ciliate Zoothamnium niveum (Bauer-Nebelsick et al. 1996; Rinke et al. 2006) had a uniaxial frond-like morphology (Kloiber et al. 2009; Fig. 1d), superficially reminiscent of the frondose Ediacaran taxa (e.g. Laflamme et al. 2004; Fig. 1d), as noted previously (McMenamin 1998). The epithelial surfaces of Zoothamnium niveum, like those of chemosynthetic phagotrophs, contain few specialized cell types and are densely covered in ectosymbionts (Bright et al. 2014). Zoothamnium actively modulates the redox conditions experienced by its thiotrophic ectosymbionts by alternately raising its frond into the water column to harvest oxygen, before returning the frond to a reclining position on the sulphide-rich seafloor (Bauer-Nebelsick et al. 1996; Bright et al. 2014). Tentative evidence for multiple impressions of a frondose Ediacaran organism are known from Newfoundland (McIlroy et al. 2009; Fig. 4a, c) and may support the role of early Ediacaran fronds as an oxygen-collecting and symbiont-hosting organ used in the same manner as the frond of Zoothamnium (Fig. 4b, c).

Fig. 4. Evidence for the use of fronds in chemosymbiosis. (a) Multiple impressions of closely associated fronds from the trace fossil bed at Mistaken Point, Newfoundland (Liu et al. 2010). Note the multiple impressions of the margin of fronds 1 and 2 and that frond 3 is anchored within the sediment, i.e. without a surficial disc. (b) Diagrammatic representation of the modern ciliate Zoothamnium, the frondose portion of which is covered in abundant thiotrophic bacteria in an ectosymbiotic relationship. (c, d) Model to demonstrate how the mode of life of Zoothamnium might apply to Ediacaran frondose rangeomorph taxa and the multiple impressions in part (a).
Conclusions

Our assessment of the mode of life of the earliest rangeomorph elements of the Ediacaran biota in Avalonia suggests the following.

(1) They were immotile diploblastic animals with a pre-placozoan grade of organization and lived below the photic zone. This is consistent with other recent arguments that suggest that the stratigraphically much younger, shallow marine Ediacaran *Dickinsonia* was of placozoan grade, had a mucociliary sole and fed on photosynthetic microbial mats using extracellular digestion (Sperling & Vinther 2010).

(2) The high surface area of the ventral surface of many elements of the oldest Ediacaran biota in southeastern Newfoundland, especially rangeomorphs such as *Fractofusus*, is most consistent with either microbial phagotrophy or the presence of extracellular or intracellular chemosymbionts. Such feeding modes are likely to have evolved from a need to supply the ventral side of immotile Ediacaran organisms with oxygen to counteract the build-up of sulphide in the pore waters beneath their bodies.

We consider that the earliest Ediacarans were animals of pre-placozoan grade that also provided oxygen to chemolithoautotrophs at their ventral surface and gained nutriment from them.

The question of where the Ediacaran biota came from, and what their precursors might have been, is one that has vexed palaeontologists for many years, especially as they appear to first arrive in the rock record as very large forms. We suggest that – given our assessment that pre-placozoan grade animals dominated the Avalon biota – there is likely to have been a phase of animal evolution in the Cryogenian plankton that included pre-adaptations for life on the seafloor, namely a means of oxygen transport, and possibly even an association with symbionts.

The modification of the sediment–water interface by the Avalonian biota represents a form of simple ecosystem engineering involving biogeochemical modification of the Ediacaran seafloor by the sessile Ediacara biota to (1) exploit sedimentary carbon and (2) avoid the build-up of sulphide below their bodies. The modification of the early seafloor by animals to create more habitable environments for themselves has been invoked for the Cambrian biotas (McIlroy & Logan 1999), but our work demonstrates that the process is likely to have begun immediately after the Cryogenian.

Our conclusion that many of the forms in the Avalonian biota may have been animals with a pre-placozoan grade of organization may, with additional work, be extended to many younger Ediacaran taxa. The younger Ediacaran sections were mostly deposited in comparatively shallow water and appear to contain an intermediate biota between the Ediacaran Avalon biota and the typical biomineralized Cambrian biotas. They include a mixture of motile and immotile organisms in ecosystems that need careful reassessment in the light of our findings.

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References

Antcliffe, J.B. & Brasier, M.D. 2007. Charnia and sea pens are poles apart. *Journal of the Geological Society, London*, 164, 49–51, https://doi.org/10.1144/0016-76492006-080

Arendt, D., Benito-Gutierrez, E., Brunet, T. & Marlow, H. 2015. Gastric pouches and the mucociliary sole: setting the stage for nervous system evolution. *Philosophical Transactions of the Royal Society, B*, 370, 20160286.

Bauer-Nebelsick, M., Bardele, C.F. & Ott, J. 1996. Redescription of *Zoothamnium niveum* (Hemprich & Ehrenberg, 1831) Ehrenberg, 1838 (Oligohymenophora, Peritrichida) a ciliate with ectosymbiotic, chemosymbiotic bacteria. *European Journal of Protozoology, 32*, 202–215.

Brasier, M.D. & Antcliffe, J.B. 2008. Dickinsonia from Ediacara: a new look at morphology and body construction. *Palaeogeography, Palaeoclimatology, Palaeoecology, 270*, 311–323.

Brasier, M.D., Liu, A.G., Menon, L., Matthews, J.J., McIlroy, D. & Wacey, D. 2013. Explaining the exceptional preservation of Ediacaran rangeomorphs from Spaniard’s Bay, Newfoundland: a hydraulic model. *Precambrian Research, 231*, 122–135.

Bright, M., Espada-Hinojosa, S., Lagkouvardos, I. & Volland, J-M. 2014. The giant ciliate *Zoothamnium niveum* and its thiotrophic epibiota *Candidatus Thio-bios zoothamnici*: a model system to study interspecies cooperation. *Frontiers in Microbiology, 5*, 1–14.

Budd, G. & Jensen, S. 2015. The origin of the animals and a ‘Savannah’ hypothesis for early bilaterian evolution. *Biological Reviews*, https://doi.org/10.1111/brv.12239

Childress, J.J. & Girguis, P. 2011. The metabolic demands of endosymbiotic chemosymbiotic metabolism on host physiological capacities. *Journal of Experimental Biology, 214*, 312–325.

Clapham, M.E., Narbonne, G.M. & Gehling, J.G. 2003. Palaeoecology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology, 29*, 527–544.

Cui, H., Kaufman, A.J. et al. 2016. Environmental context for the terminal Ediacaran biomineralization
of animals. *Geobiology*, https://doi.org/10.1111/gbi.12178

DO S REIS, M., THAWORNWATANA, Y., ANGELIS, K., TELFORD, M.J., DONOGHUE, P.C.J. & YANG, Z. 2015. Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. *Current Biology*, 25, 2939–2950.

DUBILIER, N., BERGIN, C. & LOTT, C. 2008. Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nature Reviews Microbiology*, 6, 725–740.

DUFOUR, S.C. 2005. Gill anatomy and the evolution of symbiosis in the bivalve family Thyasiridae. *Biological Bulletin*, 208, 200–212.

DUPERRON, S., NADALIG, T., CAPRAIS, J.-C., SIBUET, M., FIALA-MÉDIONI, A., AMANN, R. & DUBILIER, N. 2005. Dual symbiosis in a *Bathymodiolus* sp. mussel from a methane seep on the Gabon continental margin (southeast Atlantic): 16S rRNA phylogeny and distribution of the symbionts in gills. *Applied and Environmental Microbiology*, 17, 1694–1700.

DZIK, J. 2003. Anatomical information content in the Ediacaran fossils and their possible zoological affinities. *Integrative and Comparative Biology*, 32, 114–126.

ERWIN, D. 2015. Early metazoan life: divergence, environment and ecology. *Philosophical Transactions of the Royal Society B*, 370, 1–8.

FEDONKIN, M.A. 2003. The origin of the Metazoa in the light of the Proterozoic fossil record. *Palaeontological Research*, 7, 9–41.

FENCHEL, T. 2012. Anaerobic eukaryotes. In: ALTENBACH, A.V., BERNHARD, J.M. & SECKBACH, J. (eds) *Anoxia: Evidence for Eukaryote Survival and Paleontological Strategies*. Cellular Origin, Life in Extreme Habitats and Astrobiology, 21. Springer, Dordrecht, 3–16.

GEHLING, J.G. & NARBONNE, G.M. 2007. Spindl shaped Ediacara fossils from the Mistaken Point assemblage, Avalon Zone, Newfoundland. *Canadian Journal of Earth Sciences*, 44, 367–387.

GEHLING, J.G., DROSER, M.L., JENSEN, S.R. & RUNNEGAR, B.N. 2005. Ediacara organisms: relating form to function. In: BRIGGS, D.E.G. (ed.) *Evolving Form and Function: Fossils and Development*. Peabody Museum of Natural History, Yale University Press, New Haven, 43–66.

GRUBER-VODICKA, H.R., DIRKS, U. et al. 2011. *Paracatenula*, an ancient symbiosis between thiotrophic Alphaproteobacteria and catenulid flatworms. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 12078–12083.

HOOD, A.Y.S. & WALLACE, M.W. 2014. Marine cements reveal the structure of an anoxic, ferruginous Neo-proterozoic ocean. *Journal of the Geological Society, London*, 171, 741–744, https://doi.org/10.1144/jgs.2013-099

HOWARTH, R.W. 1984. The ecological significance of sulfur in the energy dynamics of salt marsh and coastal marine sediments. *Biogeochimie*, 1, 5–27.

IVANTSOV, A.YU. 2009. A new reconstruction of Kimberella, problematic Vendian metazoan. *Paleontological Journal*, 43, 601–611.

IVANTSOV, A.YU. 2013. Trace fossils of Precambrian metazoans ‘Vendobionta’ and ‘Mollusks’. *Stratigraphy and Geological Correlation*, 21, 252–264.

IVANTSOV, A.YU. & MALAKOVSKAYA, Y.E. 2002. Gigantiski sledy vendskikh zhivotnykh. *Doklady Akademii Nauk*, 385, 383–386.

JENSEN, S. 2003. The Proterozoic and earliest Cambrian trace fossil record: patterns, problems and perspectives. *Integrative and Comparative Biology*, 43, 219–228.

JOHNSTON, D.T., POUTON, S.W. et al. 2012. Late Ediacaran redox stability and metazoan evolution. *Earth and Planetary Science Letters*, 335, 25–35.

KLOBERG, U., PFUGGELDER-PFLANK, B., RINKE, C. & BRIGHT, M. 2009. Cell proliferation and growth in *Zoonthanum niveum* (Oligohymenophora, Petritrichida) – thiotrophic bacterial symbiosis. *Symbiosis*, 47, 43–50.

KROGH, A. 1934. Conditions of life at great depths in the ocean. *Ecological Monographs*, 4, 430–439.

LAFLAMME, M. & NARBONNE, G.M. 2008. Ediacaran fronds. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 258, 162–179.

LAFLAMME, M., NARBONNE, G.M. & ANDERSON, M.M. 2004. Morphometric analysis of the Ediacaran frond *Charniodiscus* from the Mistaken Point Formation, Newfoundland. *Journal of Paleontology*, 78, 827–837.

LAFLAMME, M., XIAO, S. & KOWALEWSKI, M. 2009. Osmotrophy in modular Ediacara organisms. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 14438–14443.

LIU, A.G., MCLROY, D. & BRASIER, M.D. 2010. First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology*, 38, 123–126.

LIU, A.G., MCLROY, D., ANTCLIFFE, J.B. & BRASIER, M.D. 2011. Effaced preservation in the Ediacaran biota of Avalonia and its implications for the early macrofossil record. *Palaeontology*, 54, 607–630.

LIU, A.G., MATTHEWS, J.J., MENON, L.R., MCLROY, D. & BRASIER, M.D. 2014. *Haootia quadriformis* n. gen., n. sp., interpreted as a muscular cnidianian impression from the Late Ediacaran period (approx. 560 Ma). *Proceedings of the Royal Society B*, 281, 20141202.

LIU, A.G., KENCHTONING, C.G. & MITCHELL, E.G. 2015. Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota. *Gondwana Research*, 27, 1355–1380.

LIU, A.G., MATTHEWS, J.J. & MCLROY, D. 2016. The *Beothukis/Calmarfrons* problem and its bearing on Ediacaran macrofossil taxonomy: evidence from an exceptional new fossil locality. *Palaeontology*, 59, 45–58.

LOENARZ, C., COLEMAN, M.L., BOLEINIGER, A., SCHIERWATER, B., HOLLAND, P.W.H., RATCLIFFE, P.J. & SCHOFIELD, C.J. 2011. The hypoxia-inducible transcriptions factor pathway regulates oxygen sensing in the simplest animal, *Trichoplax adhaerens*. *European Molecular Biology Reports*, 12, 63–70.

MCLROY, D. & LOGAN, G.A. 1999. The impact of bioturbation on infaunal ecology and evolution during the Proterozoic–Cambrian transition. *Palaios*, 14, 58–72.

MCLROY, D., BRASIER, M.D. & LANG, A.S. 2009. Smothering of microbial mats by macrobiota: implications for the Ediacara biota. *Journal of the Geological
McMenamin, M.A.S. 1998. The Garden of Ediacara. Discovering the First Complex Life. Columbia University Press, New York.

McMenamin, M.A.S. & McMenamin, D.L.S. 1990. The Emergence of Animals: the Cambrian Breakthrough. Columbia University Press, New York.

Narbonne, G.M. 2005. The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. Annual Review of Earth and Planetary Sciences, 33, 421–442.

Narbonne, G.M. 2011. Evolutionary biology: when life got big. Nature, 470, 339–340.

Narbonne, G.M. & Gehling, J.G. 2003. Life after snowball: the oldest complex Ediacaran fossils. Geology, 31, 27–30.

Pitt, K.A., Duarte, C.M., Lucas, C.H. & Uye, S. 2013. Jellyfish body plans provide allometric advantages beyond low carbon content. PLoS One, 8, e72683.

Rahman, I.A., Darroch, S.A.F., Racicot, R.A. & Lafamme, M. 2015. Suspension feeding in the enigmatic Ediacaran organism Tribrachidium demonstrates complexity of Neoproterozoic ecosystems. Science Advances, 1, e1500800.

Rinke, C., Schmitz-Esser, S. et al. 2006. ‘Candidateis Thibios zoothamnicoli’, an ectosymbiotic bacterium covering the giant marine ciliate Zoothamnium niveum. Applied and Environmental Microbiology, 72, 2014–2021.

Rosati, G. 2004. Ectosymbiosis in ciliated protozoa. In: Seckbach, J. (ed.) Symbiosis: Mechanisms and Model Systems. Springer, Dordrecht, 475–488.

Sahoo, S.K., Planavsky, N.J. et al. 2016. Oceanic oxygenation events in the anoxic Ediacaran ocean. Geobiology, https://doi.org/10.1111/gbi.12182.

Seilacher, A. 1984. Late Precambrian and early Cambrian metazoa: preservational or real extinctions? In: Holland, H.D. & Trendall, A.F. (eds) Patterns of Change in Earth Evolution. Springer, Berlin, 159–168.

Seilacher, A. 1992. Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. Journal of the Geological Society, 149, 607–613, https://doi.org/10.1144/jsigs.149.4.0607

Seilacher, A. 2007. The nature of vendobionts. In: Vickers-Rich, P. & Komarower, P. (eds) The Rise and Fall of the Ediacaran Biota. Geological Society, London, Special Publications, 286, 237–259, https://doi.org/10.1144/SP286.28

Smith, D.C. 1979. From extracellular to intracellular: the establishment of a symbiosis. Proceedings of the Royal Society, B, 204, 115–130.

Smith, C.L., Varoqueaux, F. et al. 2014. Novel cell types, neurosecretory cells, and body plan of the early-diverging metazoan Trichoplax adhaerens. Current Biology, 24, 1565–1572.

Smith, C.L., Pivovarova, N. & Reese, T.S. 2015a. Coordinated feeding behaviour in Trichoplax, an animal without synapses. PLoS One, 10, e0136098.

Smith, C.R., Glover, A.G., Treude, T., Higgs, N.D. & Amor, D.J. 2015b. Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. Annual Reviews of Marine Science, 7, 571–596.

Sperling, E.A. & Vinther, J. 2010. A placozoan affinity for Dickinsonia and the evolution of late Proterozoic metazoan feeding modes. Evolution and Development, 12, 201–209.

Thuesen, E.V., Rutherford, L.D., Brommer, P.L. & Towanda, L.T. 2005. Intragel oxygen promotes hypoxia tolerance of scyphomedusae. Journal of Experimental Biology, 208, 2475–2482.

Vinther, J. 2015. The origins of molluscs. Palaeontology, 58, 19–34.

Wood, R.A., Poulton, S.W. et al. 2015. Dynamic redox conditions control late Ediacaran metazoan ecosystems in the Nama Group, Namibia. Precambrian Research, 261, 252–271.

Xiao, S. & Laflamme, M. 2009. On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. Trends in Ecology and Evolution, 24, 31–40.