

The origin of the animals and a ‘Savannah’ hypothesis for early bilaterian evolution

Graham E. Budd^{1,*} and Sören Jensen²

¹*Palaeobiology Programme, Department of Earth Sciences, Uppsala University, Villavägen 16, SE 752 40 Uppsala, Sweden*

²*Área de Paleontología, Facultad de Ciencias, Universidad de Extremadura, 06006 Badajoz, Spain*

ABSTRACT

The earliest evolution of the animals remains a taxing biological problem, as all extant clades are highly derived and the fossil record is not usually considered to be helpful. The rise of the bilaterian animals recorded in the fossil record, commonly known as the ‘Cambrian explosion’, is one of the most significant moments in evolutionary history, and was an event that transformed first marine and then terrestrial environments. We review the phylogeny of early animals and other opisthokonts, and the affinities of the earliest large complex fossils, the so-called ‘Ediacaran’ taxa. We conclude, based on a variety of lines of evidence, that their affinities most likely lie in various stem groups to large metazoan groupings; a new grouping, the Apoikozoa, is erected to encompass Metazoa and Choanoflagellata. The earliest reasonable fossil evidence for total-group bilaterians comes from undisputed complex trace fossils that are younger than about 560 Ma, and these diversify greatly as the Ediacaran–Cambrian boundary is crossed a few million years later. It is generally considered that as the bilaterians diversified after this time, their burrowing behaviour destroyed the cyanobacterial mat-dominated substrates that the enigmatic Ediacaran taxa were associated with, the so-called ‘Cambrian substrate revolution’, leading to the loss of almost all Ediacara-aspect diversity in the Cambrian. Why, though, did the energetically expensive and functionally complex burrowing mode of life so typical of later bilaterians arise? Here we propose a much more positive relationship between late-Ediacaran ecologies and the rise of the bilaterians, with the largely static Ediacaran taxa acting as points of concentration of organic matter both above and below the sediment surface. The breaking of the uniformity of organic carbon availability would have signalled a decisive shift away from the essentially static and monotonous earlier Ediacaran world into the dynamic and burrowing world of the Cambrian. The Ediacaran biota thus played an enabling role in bilaterian evolution similar to that proposed for the Savannah environment for human evolution and bipedality. Rather than being obliterated by the rise of the bilaterians, the subtle remnants of Ediacara-style taxa within the Cambrian suggest that they remained significant components of Phanerozoic communities, even though at some point their enabling role for bilaterian evolution was presumably taken over by bilaterians or other metazoans. Bilaterian evolution was thus an essentially benthic event that only later impacted the planktonic environment and the style of organic export to the sea floor.

Key words: Cambrian explosion, ediacarans, ecology, heterogeneity, stem groups, *Kimberella*, evolution, trace fossils, animal origins, Apoikozoa.

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* Address for correspondence (Tel: +46 184712762; E-mail: graham.budd@pal.uu.se).

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I. INTRODUCTION

The transition from a Proterozoic world with benthic communities consisting of microbial mats and algae, and phytoplanktonic communities with no zooplankton into a Cambrian world with thriving benthic and planktonic animal communities raises puzzling questions about cause and effect. Several ecological mechanisms that have been suggested to be implicated – the evolution of grazing (Stanley, 1973), predation (e.g. Evans, 1912), vision (Parker, 2003) or of the mesoplankton (Butterfield, 1997) – all seem to presuppose at least some of the evolutionary events that they purport to explain: if one invokes animal innovations to explain the Cambrian explosion, one is left wondering what in turn was the ‘cause’ of the favoured innovation. For example, if one believes that the evolution of the planktonic arthropod mesoplankton had an important role in driving the Cambrian explosion, one has to account for all the evolution that needs to take place before the arthropod mesoplankton evolved, especially given that they emerged from the arthropod crustacean benthos (Rigby & Milsom, 1996). By the time of the appearance of highly derived crustaceans, one may reasonably wonder what proportion of basal animal radiation is left to be explained by their activities. These sorts of explanations also fall into the same problematic category as other ‘key innovation’ explanations (Budd, 1998) in pushing back, rather than solving the problem at hand. Rather, hypotheses are required that rely only on events that have already occurred and that do not rely on implied prescience of future conditions. That is not to deny, of course, that the innovations mentioned above were without ecological significance – rather, that their overall explanatory significance must be considered to be limited by their necessarily circumscribed nature. A further aspect to the origin of the animals, and one that has recently been under considerable scrutiny, is the role of ‘internal’ factors such as the evolution of key developmental genes (e.g. Holland, 1998, 2015) which undoubtedly played a permissive or even causal role in the evolution of key bilaterian structures and tissues such as muscle, the gut, etc. However, if these important genetic innovations are to be seen in their proper light, they must be set within an appropriate ecological framework (see e.g. Budd, 1998, 2001, for examples).

Unfortunately, many or even all key data that might be required for an understanding of the early stages in animal evolution remain highly unclear. We have as

yet a relatively poor understanding of the continental configuration at the relevant time, the composition of sea water, the carbon budget and nature and rate of carbon export from planktonic primary productivity, the phylogeny of basal animals, the affinities of many of the early fossils such as those characterising the Ediacaran Period, and indeed when the early stages of animal evolution actually took place, to name just a few. Thus, although several theories have been proposed to account for this remarkable evolutionary interval, a cautious probing of the literature reveals that the empirical basis for many of them is fragile.

A typically problematic aspect to the Ediacaran–Cambrian transition is provided by the origin of burrowing, one of the distinguishing features of the bilaterian clade. Although some cnidarians can burrow [such as the cerantharians (Jensen, 1992), actinarians (Durden, Bett & Ruhl, 2015), and sea pens], these are generally simple vertical structures [claims by Bradley (1980, 1981) of complex cnidarian burrows are problematic – see Lewy (2008) for a refutation of some of Bradley’s work], and complex and large burrows are almost certain indicators of the presence of complex anatomy including a coelom or other hydrostatic body cavity and a concentration of sensory organs (e.g. Budd & Jensen, 2000). The appearance of such burrows, probably around 545 to 543 Ma (Jensen, 2003; Mángano & Buatois, 2014) is thus the latest time that at least stem-group bilaterians could have emerged, and it is reasonable to think that the trace record before this to about 560 to 555 Ma is phylogenetically related. Even earlier traces, from the *c.* 565 Ma Mistaken Point biota, on the other hand, may have been produced by non-bilaterians (Liu, McLroy & Brasier, 2010; Liu *et al.*, 2014*b*). Why, however, would such behaviour have emerged? Burrowing is after all, very expensive energetically, even if it seems that the slow rates at which organisms burrow mitigate the cost per unit time (Dorgan *et al.*, 2011). The suggestion that organisms were driven to burrow by predation pressure (e.g. Dzik, 2007) implies the presence of mobile predators – themselves likely to be the product of the bilaterian radiation, unless the predatorial pressure came from cnidarians, adding yet another level of speculation as this would require inferences about early cnidarian feeding modes. Thus it seems necessary to take a broader phylogenetic and ecological view of the background to the bilaterian radiation, including the origin of the animals themselves.

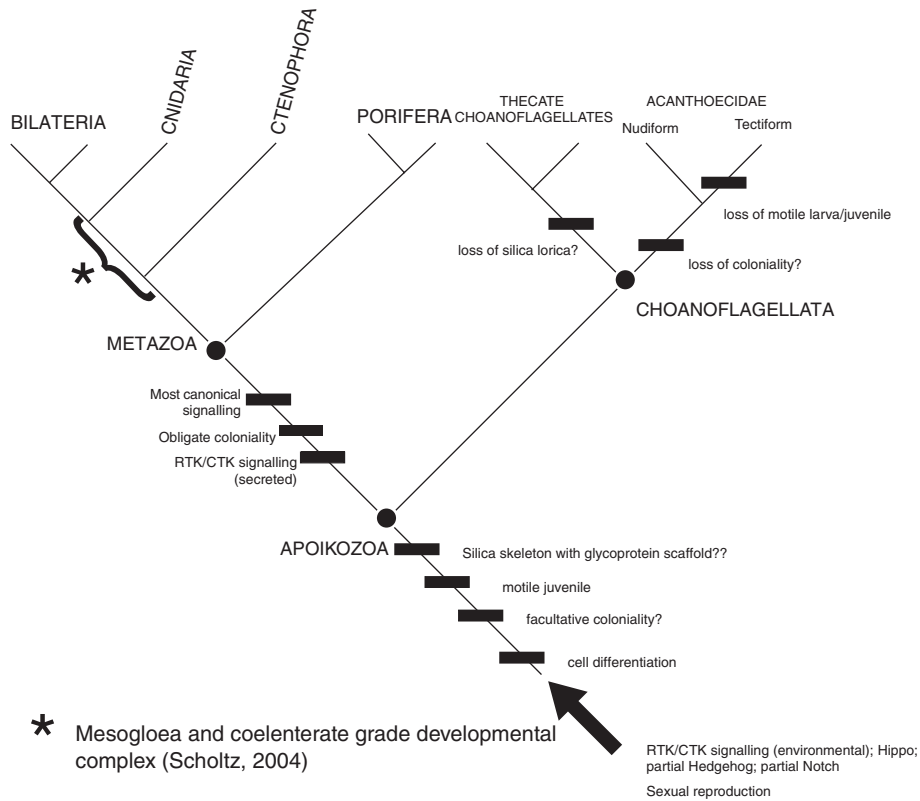


Fig. 1. One possible phylogeny of the Apoikozoa, based on Carr *et al.* (2008) and Pick *et al.* (2010). Significant early developmental and morphological features are mapped based on character optimisation between Metazoa and Choanoflagellata. Hippo, RTK/CTK (receptor tyrosine kinases/cytoplasmic tyrosine kinases), Notch and Hedgehog refer to metazoan signalling pathways. For details and data sources, see text. Placozoans omitted.

II. ANIMAL ORIGINS – THE EARLY EVOLUTION OF THE ‘APOIKOZOANS’

Animals are in the opisthokont clade of eukaryotes, i.e. a group characterised by cells bearing a single posterior flagellum (Cavalier-Smith, 1987). Other important members of this clade are the Fungi, the slime moulds, the choanoflagellates, and some other minor groups. The immediate sister group to the animals appears to be the Choanoflagellata (Carr *et al.*, 2008), followed by the Filasterea, consisting of a group of relatively little-known parasites (Cavalier-Smith, 2009). Although some information about the filastereans is available, including the presence of signalling pathways (Shalchian-Tabrizi *et al.*, 2008), most insights about the origins of the animals come from the choanoflagellates and their genome (King *et al.*, 2008) although many aspects of their ecology and genetics remain unknown. Most of the discussion below is centred on choanoflagellates and animals. Rather surprisingly, this clade does not have a commonly used name [Fairclough *et al.* (2013) use the informal name ‘Choanimal’], so we propose here *Apoikozoa*, meaning ‘colony-animals’ (Fig. 1), reflecting the widespread, and possibly basal, ability of organisms within this clade to form colonies.

Reconstruction of the last common ancestor of the apoikozoa is problematic, partly because of the continued

difficulties in reliably recovering basal animal relationships. For example, are the ctenophores basal, a sister group to the poriferans, or a sister group to the cnidarians or the eumetazoans (Wallberg *et al.*, 2004; Philippe & Roure, 2011; Philippe *et al.*, 2011)? Are poriferans mono- or paraphyletic? Are poriferans secondarily reduced or primitively simple? Where do placozoans fit in? Is bilaterality an autapomorphy of the bilaterians, or a synapomorphy of the eumetazoans? Difficult though these questions are, at least some insights can be gained by comparison with the choanoflagellates. Choanoflagellates have long excited interest because of their resemblance to the choanocytes of sponges, and many authors continue consider the two to be in some sense homologous (see e.g. Maldonado, 2004; but see also Mah, Christensen-Dalsgaard & Leys, 2014, and Section II.2). The choanoflagellates are traditionally divided into three families, although a recent phylogeny only supports one of them, the Acanthoecidae (Carr *et al.*, 2008); the other two families, the Codonosigidae and Salpingoecidae together forming a second clade. The acanthoecidans, or loricate choanoflagellates, are notable for the presence of a siliceous basket or lorica that is assembled from small costal strips, themselves assembled into costae that are arranged in a complex structure around the choanoflagellate. The function of the lorica seems to be to add stability to the

choanoflagellate whilst feeding, as the movements of the flagellum would otherwise tend to move the cell and thus reduce feeding efficiency.

The choanoflagellate costal strip is built around an inner glycoprotein core (Gong *et al.*, 2010), and in this it somewhat resembles the manufacture of the spicules of siliceous sponges. Naturally, this raises the question of whether or not the two types of structure are homologous – an obvious possibility, given their close phylogenetic proximity and shared, apparently unique bio-silica composition. However, recent discovery of a diatom-like silicic acid transport system in loricate choanoflagellates (Marron *et al.*, 2013) questions this view: these authors suggest that the ability to synthesise siliceous structures was acquired either by the loricate choanoflagellates by lateral gene transfer from diatoms, or *vice versa*. Nevertheless, the ability to transport silicic acid into the cell is not the same as the ability to utilise it, and it seems that the rest of the mechanism for producing silica in choanoflagellates differs from that of diatoms. Furthermore, although a different silicic acid transport system has been reported from a demosponge (Schröder *et al.*, 2004), none of the relevant mechanisms are particularly well known. As a result, it remains unclear whether silica production is homologous or not in choanoflagellates and metazoans (sponges), although present evidence does seem to suggest not. One further point is that members of the Ediacaran biota do not seem to preserve evidence for silica spicules or laths, and if some of these are stem-group metazoans (Section II.6), then one would expect these structures to have persisted in the stem group. Although some Ediacaran organisms, such as *Fedomia* (Serezhnikova & Ivantsov, 2007), *Coronacollina* (Clites, Droser & Gehling, 2012) and *Palaeophragmodictya* (Gehling & Rigby, 1996; Serezhnikova, 2009) have been interpreted as being spiculate, this is yet to be documented convincingly (see also Antcliffe, Callow & Brasier, 2014 for a general review of supposed Precambrian sponges including their spicules; for recent documentation of crown-group demosponges in the Cambrian, see, Botting, Cárdenas & Peel, 2015).

(1) The earliest metazoans: the placula revisited

As is well known, some of the choanoflagellates have the ability to form facultative colonies (Fairclough, Dayel & King, 2010), although these all seem to be in the planktonic rather than solitary benthic life stages. These colonies produce a jelly-like extracellular matrix that the colony is embedded in, although reports of amoebocyte-like cells in the earlier literature do not seem to have been verified. Cells in colonies of *Salpingoeca rosetta* (and other choanoflagellates) can remain connected in various ways including *via* the extracellular matrix, filopodia, and intercellular bridges (Dayel *et al.*, 2011). The intercellular bridges are reported to resemble the products of incomplete cytokinesis seen in metazoans (e.g. in germ cysts; Ong & Tan, 2010) and perhaps also the plugged cytoplasmic bridges seen in hexactinellids (Leys, 2003). It is therefore possible that the last common ancestor of animals and choanoflagellates was able to form colonies (see Carr *et al.*, 2008, who argue that coloniality must have

appeared early in choanoflagellate evolution, and cannot be ruled out as a possible synapomorphy of choanoflagellates and metazoans), complete with extracellular matrix (ECM) (for reviews of the evolution of the ECM, see Hynes, 2012; Adams, 2013). We would nevertheless caution that although this is one possible reconstruction given the available evidence, it does require loss of this ability in one of the extant clades of choanoflagellates, the Acanthoecidae (Fig. 1).

While traditionally the earliest animals are regarded as being planktonic, the phylogenetic evidence is not decisive (existing choanoflagellate colonies are planktonic; those of animals are benthic). This is a timely reminder that the living choanoflagellates are themselves derived relative to their last common ancestor with living animals, a point that Brasier (2009) emphasised with regard to cnidarians. However one good reason for concluding that stem-group animals were benthic is their large size: such benthic colonies – probably also with the ability to (at least facultatively) produce differentiated cells (as do choanoflagellates, albeit not in colonies; Dayel *et al.*, 2011) – might best be considered as competitors within the general ‘mat-world’ setting of the later Proterozoic. They would have thus grown larger colonies in order to avoid being overgrown by their microbial competitors (see comments in Reitner & Wörheide, 2002). This view is decidedly in contrast to the Haeckelian heritage of undifferentiated planktonic balls of cells giving rise to the earliest metazoans (e.g. Nielsen, 2008). It places stem-group metazoans in a competitive microbially dominated benthos and not the plankton, and includes the early appearance of cellular differentiation before colony formation (Mikhailov *et al.*, 2009). It partly parallels the early stages of the ‘placula’ theory of Bütschli (1884) [see also a general review of theories of animal evolution by Mikhailov *et al.* (2009)], and also in important aspects the ‘synzoospore’ theory of Zakhvatkin (1949). Of particular interest here is the intimate association of sponges with various prokaryotes, which may be important in their feeding modes (Yahel *et al.*, 2003; Maldonado, 2007), including demosponges with eubacteria (Schumann-Kindel *et al.*, 1997) and hexactinellids with archaeans (Thiel *et al.*, 2002). These can be transferred during reproduction (Kaye, 1991), giving the impression of sponges being in some regards differentiated parts of microbial mats. Indeed, the role of bacteria in facilitating early animal evolution may be significant (Alegado *et al.*, 2012; for a useful review, see Alegado & King, 2014). The early animals may have increased their genetic armoury directly *via* lateral gene transfer from their prey, and by co-option of adherence proteins involved in prey capture into the mechanism for multicellularity. Furthermore, specific chemical cues from bacteria can trigger the formation of multicellular colonies in choanoflagellates (Alegado *et al.*, 2012). Such subtle reciprocal interactions with their prey may explain how the animals rose to be so complex, and why it took them so long to do so.

If this general view of sponges (and other animals) evolving *via* biofilms from a colonial opisthokont is correct, then it seems likely that these animals were capable of feeding

on bacteria and/or dissolved organic carbon (DOC), as do choanoflagellates (Gold, Pfister & Liguori, 1970) and sponges (Alegado & King, 2014). Given the general presence of sexual reproduction in eukaryotes and in particular in animals, and the likelihood of sexual reproduction in choanoflagellates based on the presence of meiosis genes (Carr, Leadbeater & Baldauf, 2010 – even if sexual reproduction has never been observed directly), these stem animals and eumetazoans were also likely to reproduce sexually, and thus to have at least a mobile sperm stage. In some sponges, this is the only motile life stage, but others also have motile larval and juvenile stages (Maldonado, 2004, 2006) and adult sponges are known to be capable of slow movement (Bond & Harris, 1988). The peculiar mode of fertilization in some sponges, whereby the sperm is captured by a choanocyte, which in turn ferries it to the oocyte (Simpson, 1984; Maldonado & Riesgo, 2008), may reflect reproductive strategies in now-extinct more-basal taxa. Thus, mobility at some level was present as a plesiomorphy for Metazoa, and indeed Apoikozoa. Given the relatively complex lifestyles of even unicellular opisthokonts, it is perhaps not surprising that they have a set of signalling pathways that in at least some aspects shadow the canonical eight developed more fully in metazoans and especially bilaterians (Pires da Silva & Sommer, 2003; King *et al.*, 2008; Shalchian-Tabrizi *et al.*, 2008; Seb -Pedr s *et al.*, 2012; Fairclough *et al.*, 2013), although it is also clear that considerable evolution of signalling pathways has taken place independently in choanoflagellates and metazoans (e.g. Suga *et al.*, 2008), and the suggestion that choanoflagellates essentially possess animal-like pathways would be misleading. Finally, it is likely that these early metazoans were characterised by a substantial collagenous ECM that would have provided support for large colonies (Adams, 2013).

(2) Basal animal relationships

Although several analyses (e.g. Sperling, Pisani & Peterson, 2007) have suggested that the sponges are paraphyletic, some recent phylogenies have recovered more traditional groupings, with a monophyletic Porifera and ctenophores either as sister group to the cnidarians (thus reviving the traditional Coelenterata) or in an unresolved trichotomy at the base of the Eumetazoa (Philippe *et al.*, 2009, 2011; Budd, 2013; Nosenko *et al.*, 2013). Thus, at present, the conclusion must be that we have not yet fully resolved basal animal relationships. In reconstructions where sponges are monophyletic, the eumetazoans need not be derived directly from a sponge, complete with supposedly sponge-specific apomorphies such as the water canal system; but the presence of choanocytes as cell types in sponges rather strongly suggests that both stem-animals and eumetazoans were at least somewhat sponge-like in organisation, assuming their homology with choanoflagellates (for skeptical voices concerning the homology of choanocytes and choanoflagellates, see Mah *et al.*, 2014). Note also that choanocyte-like cells are phylogenetically widely scattered, including in deuterostomes and other protists (e.g. Maldonado, 2004;

Mah *et al.*, 2014, and references therein), although these are not generally considered to be homologous).

The possibility of the ctenophores being the sister group to the rest of the animals (Dunn *et al.*, 2008, 2014; Ryan *et al.*, 2013; Moroz *et al.*, 2014; but see also Philippe *et al.*, 2009; Pick *et al.*, 2010; Nosenko *et al.*, 2013) remains surprising. For example, genomic analysis (fig. 3 in Moroz *et al.*, 2014) suggested that ctenophores have a highly reduced complement of metazoan genes. However, these may not be primary, but secondary absences (see also Copley *et al.*, 2004), a possibility that could be investigated by comparing the gene complement of, for example, bilaterians and choanoflagellates. Various lines of evidence, especially the genome analysis of Ryan *et al.* (2013), suggest that not only are ctenophores basal, but their nervous system and/or mesoderm may be convergently derived relative to that of bilaterians (Dayraud *et al.*, 2012; Moroz *et al.*, 2014; Ryan, 2014; see Steinmetz *et al.*, 2012 for similar arguments about the convergence of striated muscle in cnidarians and bilaterians). There is also the suggestion that the presence of nerve tissue-specific genes shared by ctenophores and sponges might conversely suggest the loss of a nervous system in sponges (for a review of whether sponges can be considered to have a nervous system, see Nickel, 2010). The principal difficulty with using molecules as markers for homology, as has been argued for both muscles and nerves, is that a morphological structure may be homologous between two taxa and yet have diverged at the molecular level (see e.g. Budd, 2013, for the case of segmentation patterning in insects). Given the morphological similarities between the muscles of cnidarians and bilaterians, for example, and their sister-group relationship, we can still consider the two as being homologous, despite their molecular divergence. Similarly, the synaptic nerves of ctenophores, which also share a number of molecular markers with eumetazoans (Ryan, 2014) do not need to be seen to be convergent, despite also possessing marked differences at the molecular level: homology is not the same thing as similarity [see Marlow & Arendt (2014) for a defence of nervous system homology in ctenophores and other animals, and Monk & Paulin (2014) for a general review of the early evolution of neurons].

No matter what phylogenetic reconstruction is eventually adopted, the conventional view of early animal evolution marching confidently through cell grade (sponges) to tissue grade (cnidarians, ctenophores) to organ grade (bilaterians) seems to be shaken by hints of a more complex pattern of gain, loss and convergence (Ryan *et al.*, 2013). If ctenophore systems are homologous to those of eumetazoans, and they are basal, conversely, then a monophyletic Porifera may be secondarily (and rather profoundly) reduced. Nevertheless, sponges, far from being the more or less featureless blobs of conventional wisdom, are emerging to be more eumetazoan-like than previously supposed. For example, some appear to form closed epithelia with a basement membrane (Boute *et al.*, 1996; Adams, Goss & Leys, 2010; Ereskovsky, Renard & Borchiellini, 2013) and can propagate contractile waves through their tissues

(Leys, 2003). The phylogenetic distribution of such features throughout sponges remains somewhat unclear partly because they remain poorly studied. Recent studies (e.g. Maldonado, 2004) have shown that the newly recognised class *Homoscleromorpha* possesses polarised pinacoderm cells with eumetazoan-like basement membranes in both adults and larvae, essentially meaning they have true epithelia. By contrast, adult sponges of other clades possess poorly polarised cells in their pinacoderm or outer covering, and lack a collagenous basement membrane, so that the cells are free to migrate in and out of the underlying mesohyl (Maldonado, 2004). There are at least hints that other sponge larvae may also harbour something approximating basement membranes (Vacelet, 1999; Maldonado, 2004). The significance of such observations depends very much on the phylogenetic arrangement of sponges, and whether this is simply a convergence or not. If they are monophyletic with homoscleromorphs plus calcareans as the sister group to all other sponges (Philippe *et al.*, 2009), then one suggestion would be (by comparison to a eumetazoan outgroup) that all sponges originally possessed true epithelia, which have been lost in most clades. If so, then crown-group sponges may differ significantly from stem-group forms, which may be expected to be much more constrained by the presence of epithelia. Conversely, this reconstruction makes the idea of sponges simply being large choanoflagellate colonies untenable, for it is based on crown-group sponges that may be more colony-like than their direct ancestors. Nevertheless, the significance of these speculations should not be over-rated: homoscleromorph sponges are still extremely sponge-like, despite their epithelia.

The potential problems of saturation, inadequate models, long-branch attraction and taxon undersampling combine to make the position of the ctenophores very uncertain (Nosenko *et al.*, 2013). In the face of this molecular uncertainty, we do not consider the traditional view of ctenophores as forming part of a clade consisting of cnidarians, ctenophores and bilaterians (with or without placozoans) to have been falsified (see e.g. comments in Simion *et al.*, 2015). Our inability to resolve basal animal relationships exerts a strong and confounding effect on our understanding of the early fossil record. For example, if 'sponges' are really paraphyletic, then in order to reach the last common ancestor of cnidarians or bilaterians, one would necessarily have to pass through a crown-group 'sponge' ancestor. This would in turn imply that before the first bilaterian animals and their fossils evolved, sponges must have diversified greatly: the stem groups at least of all their major lineages must have been established by then. The remarkable silence of the Precambrian fossil record on the topic of sponges, and their proliferation, both as body fossils and isolated spicules, in the Cambrian, may be telling. It is possible, as discussed by Sperling *et al.* (2010) and Sperling, Peterson & Laflamme (2011), that Precambrian sponges were simply 'different' from Phanerozoic ones, but this suggestion – which requires that that modern sponges have independently acquired their distinctive morphology from a very different

ancestor – seems to be somewhat unlikely. If ctenophores are the sister group to cnidarians plus bilaterians, then the old characters that used to unite the 'Coelenterata' would become plesiomorphies that would characterise the lineages that gave rise to both cnidarians and indeed bilaterians. This would, like the 'sponges first' scenario above, provide a useful indicator for what these animals might look like. In reconstructions where ctenophores and cnidarians form successive offshoots to the bilaterians (e.g. Pick *et al.*, 2010), potential plesiomorphies of ctenophores and cnidarians such as the presence of the mesoglea, muscles and nerves, thus become important in assessing the potential morphology of stem-group animals. Conversely, if ctenophores are an independently derived clade at the base of the tree, then we have few indications about the transition from the metazoan last common ancestor to ctenophores, and from the last common ancestor of sponges with the eumetazoans to the eumetazoans themselves. This basic uncertainty must undermine our confidence in understanding the early fossil record of the period in question, to which we now turn.

We wish to stress, in line with our previous work (Budd & Jensen, 2000; Budd, 2013), that there is no reason to prioritise crown- over stem-group animals. Just like crown-group animals, members of the deep stem groups in question had definite features, some of which were undoubtedly retained by extant crown groups. For example, even if ctenophores had a long stem group with the crown group evolving relatively recently (Podar *et al.*, 2001), their ancestors were not featureless. A consequence of this is that characters associated uniquely with modern monophyletic clades almost inevitably had a broader distribution in the past than they do now. Conversely, it is worth stressing that the absence of particular features of modern clades does not exclude an organism from the relevant total group. These points will become relevant when we begin to consider the problematic early putative animal fossil record.

In order to make sense of the fossil record, it is necessary to have a working model of animal phylogeny (albeit one incorporating potential flexibility), so we have chosen to use the tree of Pick *et al.* (2010) as our framework (Fig. 1), i.e. with a monophyletic basal Porifera, and Ctenophora as sister group to Cnidaria + Bilateria, which we believe is the best-supported current topology (see Ryan *et al.*, 2010). The position of the Placozoa is not relevant to our argument. This tree is consonant with sponges and choanoflagellates having arisen from an at least facultatively colonial ancestor, and highlights the importance of the ECM persisting up the stem groups to Eumetazoa and Bilateria [homology between Cnidaria and Ctenophora remains uncertain, however, largely because of the poorly studied nature of the ctenophore ECM (Adams, 2013)]. In addition to a well-developed ECM, other potential features present in these stem groups would include an oral–aboral axis and some early developmental similarities identified by Scholtz (2004). The recent description of the problematic *Dendrogramma* (Just, Kristensen & Olesen, 2014) may provide some indications of the sorts of organisms this set of characters might correspond to. Finally,

this phylogeny would suggest that the classical Epitheliozoa (that is, Cnidaria + Placozoa + Ctenophora + Eumetazoa) primitively were predators.

(3) The earliest fossil record of the apoikozoans

The fossil record of the earliest stages in apoikozoan evolution remains lamentably poor. The oldest fossils that might be relevant to the basal apoikozoans are probably the oldest ‘Ediacara’-aspect taxa at around 579 Ma from the Avalonian assemblage (Narbonne & Gehling, 2003; Narbonne, 2005; Liu *et al.*, 2012) and thus post-dating the Gaskiers glaciation at around 583 Ma. The so-called ‘Twitya disks’ from the Canadian Cordillera are even older as they date from before the Marinoan glaciation, but their simplicity makes further comparison with extant taxa difficult (Narbonne, 2007). Apparently similar forms have been reported from the >750 Ma Kurgan Formation of Kazakhstan (Meert *et al.*, 2011) and the Mesoproterozoic Sukhoy Pit Group of East Siberia (Liu *et al.*, 2013); again, their relevance to metazoan evolution remains unclear. The Lantian biota (Yuan *et al.*, 2011, 2013) seems to consist largely of algae, but the description of one of the more complex taxa as a possible conulariid-like organism (probable cnidarians known otherwise from the Palaeozoic) is not without interest (Van Iten *et al.*, 2013). The dating of the Lantian however, remains somewhat uncertain and it may in fact post-date the Gaskiers glaciation at *c.* 580 Ma, although it has been claimed to be immediately post-Marinoan at *c.* 630 Ma (Yuan *et al.*, 2011). As is common with singular identifications (Budd, 2013), if one cnidarian is found in such early deposits, it implies that a considerable amount of early animal evolution had taken place by then. Nevertheless, the case for late-Precambrian total-group cnidarians is beginning to build, for example with the recent description of a potentially cnidarian-like form, *Haootia quadriformis* from Newfoundland at *c.* 560 Ma, complete with putative muscle (Liu *et al.*, 2014a; Liu, Kenchington & Mitchell, 2015), although this specimen is perhaps too poorly preserved for a definitive judgement.

(4) Late Ediacaran macroscopic fossils: systematics and taxonomy

Probably no other fossils have generated such a range of diverse interpretations as the enigmatic ‘Ediacaran’ macrofossils from the late Ediacaran Period, with possibly the only broad agreement being the absence of biomineralized hard parts. For example, views on the affinities of archetypical late Ediacaran fossils such as *Dickinsonia* have varied between considering them more or less conventional members of known phyla (e.g. Glaessner, 1984; Gehling, 1991; Sperling & Vinther, 2010; Gold *et al.*, 2015), and regarding them as fungi, algae, xenophyophores, lichens, etc. (e.g. Seilacher, 1984, 1999; Retallack, 1994; Peterson, Waggoner & Hagadorn, 2003). Of these, the most influential and provocative has been the ‘Vendobionta’ theory of Seilacher (e.g. Seilacher, 1984; Seilacher & Gishlick, 2015), which at least as originally conceived saw the Ediacarans as

flattened organisms constructed from a characteristic ‘pneu’ (i.e. airbed) structure, with no phylogenetic relationships to metazoans but rather being protists. Conversely, an intermediate view that we continue to support here sees them as animals, but not as members of crown groups of living phyla (e.g. Budd & Jensen, 2000; Dewel, 2000; Dewel, Dewel & McKinney, 2001; Zhu *et al.*, 2008; Section II.6).

Genus-level classification appears to be the most used, and perhaps most useful, level of communication with regards to these fossils. Here we briefly examine problems in higher-level classification of these fossils and consider some recent systematic studies in which a substantial body of Ediacara-type fossils have been considered to be animals. The search for affinities with Phanerozoic animals is complicated by the absence of readily identifiable anatomical features, and in cases where these have been reported, such as the purported intestine in *Dickinsonia*, they are subtle features for which alternative interpretations are invariably offered. It would also be desirable to know if the absence of readily identifiable anatomical detail is a taphonomical artefact. This question remains largely open. Information on the extent to which anatomical detail of modern soft-bodied animals would be preserved during fossilisation would also be of interest, but such information is limited. Finds of Ediacara-type fossils preserved both as carbonaceous films and the more typical mouldic preservation in sandstone (Xiao *et al.*, 2013) may eventually provide insights but the number of taxa remains low. There is also uncertainty in whether the available fossils represent the whole organism or only a part. Many discoidal fossils are known to have formed the base for frond-like erect structures, but this may not apply in all cases. Some fractal genera may represent ontogenetic (or ecological?) series (Brasier & Antcliffe, 2004) and this may also apply to other specimens – Grazhdankin (2014) noted that *Parvancorina* and *Temnoxa* show similarities to parts of *Kimberella*. The degree of preserved information, although often hard to evaluate, differs across the range of Ediacara-type fossils. Some forms show a more complex morphology. *Spriggina* has been considered by many authors (e.g. Gehling, 1991) as a promising candidate with affinities to either arthropods or annelids but definite proof has not yet been obtained. Presently, *Kimberella* arguably provides the most diverse range of morphological detail, but even so its placement remains in doubt (Section II.5). Speculation on the phylogenetic relationships of, and among, Ediacara-type fossils is largely based on general features such as symmetry and polarity. Radially symmetrical forms, when interpreted as animals, have generally been considered cnidarians (or coelenterates), although attempts to place them into modern classes have not been successful. As emphasised by Brasier (2009), attempts at direct comparisons between what were likely stem-group cnidarians and Phanerozoic cnidarians may in any case be futile as they evolved under very different ecological conditions.

Recent attempts at supra-generic classifications have been made by Erwin *et al.* (2011) and Grazhdankin (2014). Before considering these schemes it is relevant to mention

an earlier and relatively comprehensive supra-generic classification by Fedonkin (e.g. 1985, 1987), who interpreted Ediacara-type fossils as animals but with the majority placed in classes that left no descendants. His Cyclozoa and Inordoza represent morphologically simple and more complex classes of coelenterates, respectively. Also attributed to the Coelenterata is Trilobozoa, forms with three-rayed symmetry. Still other forms were considered likely colonial coelenterates, the Petalonamae, with families Erniettidae and Pteridinidae. A variety of bilaterally symmetrical forms such as *Dickinsonia* and *Vendia* were considered to be bilaterian animals of the Phylum Proarticulata. Other genera were considered more or less closely related to Phanerozoic animals. This classification scheme has not been widely adopted outside of the former Soviet Union.

As with Fedonkin's classification body symmetry is an important characteristic in the schemes of Erwin *et al.* (2011) (see also Xiao & Laflamme, 2009; Laflamme *et al.*, 2013) and Grazhdankin (2014), with importance placed on branching and segment nature. Erwin *et al.* (2011) recognized six units that they considered to be clades: Rangeomorpha, with self-repeating modular units; Arboreomorpha, with primary branches stitched together into large leaf-like sheets; Kimberellomorpha, including *Kimberella*; Erniettomorpha, modular organisms; Dickinsoniomorpha, modular organisms, with a suggestion of shrinkage and movement; and Triradialomorpha, with three planes of symmetry. In addition to these clades, they also recognized three other possible clades of bilateriomorphs, bilaterally symmetrical forms with anterior–posterior differentiation, tetradialomorphs and pentaradialomorphs. Most of these groups are considered to be megascopic organisms of unknown affinities. Only Kimberellomorpha are considered members of a crown-group phylum, and Dickinsoniomorpha are considered likely animals. For both Kimberellomorpha and Dickinsoniomorpha, the association of body fossils with their supposed trace fossils has been used as an argument for their being within Metazoa. At least with respect to *Dickinsonia* this seems unsubstantiated: in Seilacher's (e.g. Seilacher & Gishlick, 2015) view, these fossils simply provide evidence for movement in one vendobiont.

In the scheme of Grazhdankin (2014) eight high-level taxonomic groups are attributed to three major clades. The Vendobionta, with no relationship to the Eumetazoa, are forms with serial or fractal quilting and comprise the Rangeomorpha, Dickinsoniomorpha, and Petalonamae. The Frondomorpha are frond-shaped forms with a discoidal holdfast. Tribrachiomorphs and bilateriomorphs are considered eumetazoans.

There are obvious general similarities between the above classifications although they differ in detail. For example in the scheme of Fedonkin (1987), *Spriggina* is possibly an arthropod, in that of Erwin *et al.* (2011) it is a bilateriomorph, whereas in that of Grazhdankin (2014) it is a dickinsoniomorph.

These classification schemes are valuable in that they make claims for what may be natural groups, and so direct

attention to their evaluation. But although both Erwin *et al.* (2011) and Grazhdankin (2014) present their classifications in terms of phylogenetic systematics, it is important to recall that these are morpho-groups. Features that are presented as being synapomorphies in these classifications could well be homologous – but without known sister-group comparisons and character polarity, claims for synapomorphies cannot be made, and it is erroneous to describe several of the above groups as clades or monophyletic clades. Our understanding of Ediacara-type fossils is still at a stage where the primary task must be a search for homologous structures and we therefore do not rely heavily on the above classification schemes.

Apart from their affinities, other controversial aspects of the Ediacarans are the extent to which they exhibit biogeographical differentiation, and the degree to which the different forms can be stratigraphically resolved. Waggoner (1999) recognised three assemblages, the Avalonian, White Sea and Nama, and found that they formed a temporal succession, with the Avalonian assemblage being the oldest. The oldest 'Avalonian' assemblages essentially consist of 'fractal' forms that make up the Rangeomorpha; the middle, 'White Sea' assemblages contain many classical Ediacaran taxa such as *Spriggina* and *Dickinsonia*; and the youngest 'Nama' assemblage is a rather low-diversity assemblage of forms such as *Swartpuntia* and *Ernietta*, and also contains the earliest biomineralized animals such as *Cloudina*. It later became apparent that Waggoner's (1999) assemblages also represented different environments, raising the possibility that their apparent temporal succession was controlled by changing facies rather than being a true stratigraphical succession (Grazhdankin, 2004, 2014; Gehling & Droser, 2013). For example, in the area around Ediacara itself, elements of all three of these assemblages were found in the Ediacara Member of the Rawnsley Quartzite Formation (Gehling & Droser, 2013). Although the pattern is clearly more complex than a simple non-overlapping three-fold biozonation, it still holds true that the youngest and oldest known assemblages are highly distinct (fig. 7 in Grazhdankin, 2014). The earliest assemblages still consist almost entirely of fronds and fractal forms (i.e. members of the Rangeomorpha), whereas the youngest contain a low diversity of forms such as *Pteridinium*, *Ernietta* and *Swartpuntia*, together with the frondomorph *Charniodiscus* (Grazhdankin, 2014). Thus, relative to the original formulation of Waggoner (1999), the three zones are somewhat telescoped together, although they can still be distinguished.

Here we consider the 'Ediacarans' to consist of the classical taxa known from South Australia, Namibia, the White Sea, Avalonia, etc., excluding trace fossils, obvious algae and organisms with hard parts. In principle, if the relationships between the Ediacarans can be clarified, and one or more characters can be found to relate at least one of them to an extant group, then we might achieve a greater understanding of the role Ediacarans potentially played in animal evolution.

One difficulty in understanding Ediacaran relationships arises from the concentration of studies on only one or

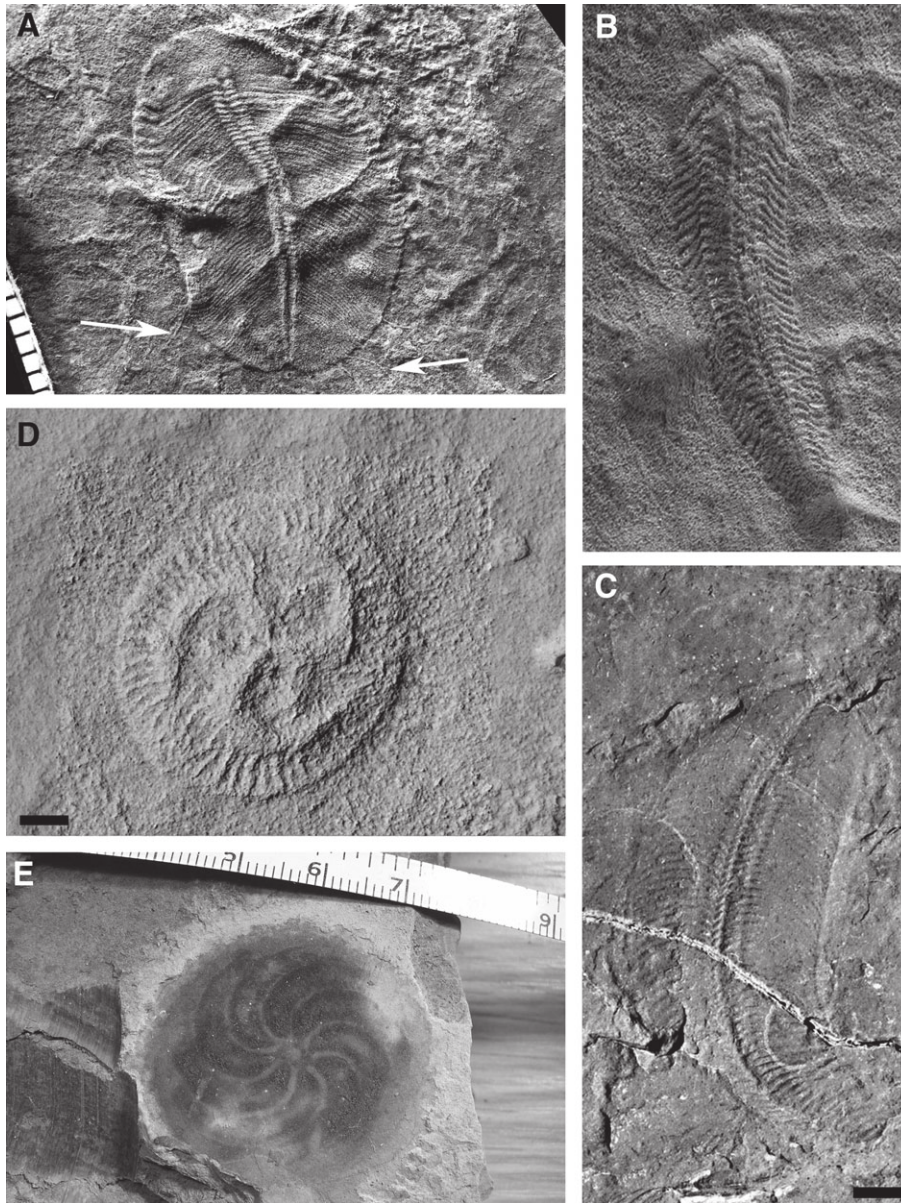


Fig. 2. Selected Ediacaran fossils. (A–C) Note their constructional similarities as potential homologies, especially the asymmetrical ‘head’ regions, the axial paired offset repeated structures, the flanking repeated structures and marginal structures. (A) *Iovicia rugulosa* (thread-like structures from posterior indicated by arrows). (B) *Spriggina floundersi* (F17354; cast in Cambridge, UK). (C) *Pteridinium simplex* (field photograph). (D, E) Two possible stem-group ctenophores. (D) *Tribrachidium heraldicum* (Holotype SAM P12898; cast in Cambridge, UK). (E) *Eoandromeda octobrachiata* (JK10903 from Tang *et al.*, 2008). Scales: mm scales in (A–C, E); scale bar, 2 cm in (C), 2 mm in (D). Photo credits: (A) Andrej Ivantsov; (B) Jim Gehling; (C) S. J.; (D) Martin Smith; (E) Stefan Bengtson.

two forms. *Dickinsonia* has probably been the subject of most speculations about its affinity, including such highly surprising claims as its being a lichen (e.g. Retallack, 2007). Understanding one form will always be problematic in the absence of a broader consideration of related taxa, which may show wide variation in morphology. At least some Ediacarans seem to be clearly related, at least in terms of shared morphological features. For example, the various rangeomorphs – e.g. *Bradgatia*, *Fractofusus*, *Rangea*, *Charnia*, etc., show pronounced similarities (Brasier & Antcliffe, 2004;

Laflamme *et al.*, 2013). Similarly, some of the fronds and broadly bilateral forms are also likely to be related. For example, *Spriggina* (Fig. 2B) shows an asymmetric ‘head’ region, a double axial row of offset structures, and abaxial features with pronounced geniculation. All these structures are found in *Iovicia rugulosa* (Fig. 2A – see Ivantsov, 2007), and to a greater or lesser extent in *Yorgia waggoneri* (Fig. 3), *Dickinsonia lissa*, *Swartpuntia*, *Archaeaspinus* (Fig. 4A) and *Marywadea* (among others, such as perhaps *Pteridinium*, Fig. 2C), many of which are grouped in Fedonkin’s ‘Proarticulata’



Fig. 3. *Yorgia waggoneri* from Nilpena, Australia (resin reconstruction SAM P40110; South Australia Museum), showing the apparent marginal diverticulae (arrow). Scale bar, 10 mm. Photo: Jim Gehling.

(Fedonkin, 1985). We regard these similarities to be good candidate homologies (Fig. 2A–C). However, as Gehling *et al.* (2005) remark, merely pointing out similarities may disregard important differences. For example, *Dickinsonia* (Fig. 4B, E) seems to be a highly flexible (and indeed contractile, e.g. Gehling *et al.*, 2005) organism, whereas taxa such as *Pteridinium* and *Spriggina* seem to be more well defined or even somewhat rigid (although this may be overemphasised – see e.g. Grazhdankin & Seilacher, 2002, for preservation of *Pteridinium* showing high flexibility). If these organisms are related, then they clearly display a certain degree of diversity.

The relationships between the various fronds are also controversial. For example, it has been suggested that the ‘fractal’ forms such as *Charnia* are unrelated to at least some *Charniodiscus* (Laflamme *et al.*, 2013; D. Grazhdankin, personal communication). The genus *Charniodiscus* itself seems to be heterogeneous (J. Cuthil Hoyall, personal communication; J. Antcliffe, personal communication), but at least some do not appear to show the characteristically divided branches seen in *Charnia*. Nevertheless, Brasier & Antcliffe (2004) and Brasier, Antcliffe & Liu (2012) imply with transformational series that all these forms may be related.

Perhaps the most interesting recent suggestion of Ediacaran affinities was based on *Eoandromeda* (Fig. 2E), which was described as a stem-group ctenophore or coelenterate (Tang *et al.*, 2008, 2011; Zhu *et al.*, 2008; Xiao *et al.*, 2013) from the Doushantou Formation of South China and from the Ediacara Member of South Australia. This taxon is

of great interest as it has been found both in the typical Ediacara-type preservation as moulds and casts in relatively coarse sediments, and also as flattened carbonaceous films, more like the exceptional preservation in Lower Palaeozoic *lagerstätten*. This is important as it confirms that the unusual preservation at the base of sandstone beds is due to particular taphonomic conditions rather than unique organism properties. *Eoandromeda* possesses eight spiralling arms that seem to be attached to a globular body, and which are characterised by dark transverse lines; at the apex of the organism, the arms appear to be linked into a small ring-like structure. Taken together, these features suggest affinities with ctenophores, with the dark transverse lines potentially representing ctenes. Remarkable ctenophore embryos have been described from the basal Cambrian of China (Chen *et al.*, 2007) that show very similar structures, including, critically, the annular structure at the apex. Note that extant ctenophores, rather than being biradially symmetrical as traditionally described, also show elements of rotational symmetry (e.g. Martindale & Henry, 1999). This reconstruction suggests affinities with taxa such as *Tribrachidium* (Fig. 2D; Glaessner & Daily, 1959) and *Albumares* (Keller & Fedonkin, 1977). It is possible to compare *Tribrachidium* to some of the so-called bilateralmorph taxa such as *Ivovicia rugulosa* (Fig. 2A; Ivantsov, 2004). These typically do not show bilateral symmetry, with the exception of some specimens of *Dickinsonia*, instead showing a staggered pattern between the sides of the annulations of the body; further, the ‘head’ region also shows a striking asymmetry, and we tentatively suggest that these head regions are comparable to a pair of the three branch-like structures seen in the centre of *Tribrachidium* (Hall *et al.*, 2015). Nevertheless, at least some specimens of *Dickinsonia costata* do show the annulations clearly crossing the midline unbroken (e.g. fig. 6 of Gehling *et al.*, 2005). Can these differences be reconciled? One possibility is that the upper and lower surfaces of *Dickinsonia* differed, with one symmetrical and one asymmetrical; we explore this possibility further below.

Although Ediacara-type organisms have often been depicted as relatively flat forms it is evident that this was not the case for the vast majority (e.g. Gehling *et al.*, 2005). One relatively neglected feature of Ediacarans is the presence of apparent internal body cavities, for example in the remarkable specimens of *Dickinsonia* illustrated by Dzik & Ivantsov (2002), Ivantsov (2004) and Zhang & Reitner (2006) (see plate 101 and fig. 4 in Glaessner & Wade, 1966, and discussion in Jenkins, 1992) with an apparent set of branching diverticulae of relatively consistent form, and a broad central structure described as a pharynx (Fig. 4B), which may be similar to structures seen in taxa such as *Paravendia janae* and *Vendia rachinata* (Fig. 4C, D; Ivantsov, 2004). Although these features have been considered by some to be merely contractional wrinkling (Gehling *et al.*, 2005) or even characteristic features of lichens (Retallack, 2007), their relatively consistent form and symmetry within the body suggests that they reflect true structures; the three-dimensional features in taxa such as *Vendia* and *Paravendia* are very unlikely to be preservational artefacts. Potential internal canals or diverticulae are also seen

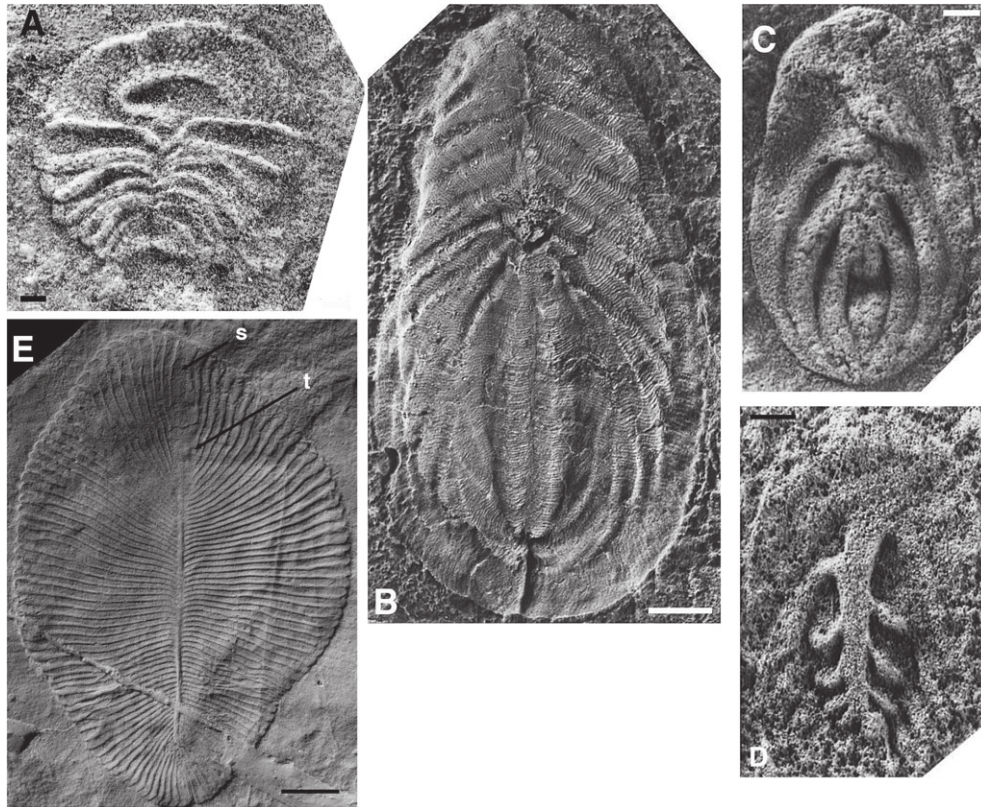


Fig. 4. Selected Ediacaran fossils. (A) *Archaeaspinus fedonkini* (PIN 3993/5053), (B) *Dickinsonia* sp. (PIN 3993/5173), (C) *Paravendia janae* (3993/5070), (D) *Vendia rachiata* (PIN 4853/63), (E) *Dickinsonia costata* (F17462; Wade, 1972). Panels (A–D) are from the White Sea area; (E) from the Ediacara area. Scale bars: (A, C, D) 1 mm; (B) 5 mm; (E) 20 mm. Photo credits: (A–D) Andrej Ivantsov; (E) Martin Smith. In (E) ‘s’ indicates the ‘spatulate’ low-resistance segment of Brasier & Antcliffe (2008); ‘t’ shows the region considered a pharynx by e.g. Jenkins (1992): note, however, its possible similarity to the terminal structure in *Kimberella* (see Fig. 5A).

in *Yorgia wagonneri* (Fig. 3; Ivantsov, 1999), *Anfesta stankovskii* (Fedonkin, 1984) and *Albumares brunsae* (Keller & Fedonkin, 1977), as well as *Cyanorus singularis* (Ivantsov, 2004), the latter of which seems to show both external rugosity and internal branching structures (plate 1 and figs 1–6 in Ivantsov, 2004; see also discussion in Dzik & Martyshyn, 2015).

The presence of branching internal channels has implications for the constructional morphology of these taxa. For example, the organisms do not seem to be of a simple ‘air-bed’ construction made of a single set of inflated modules, as the channels seem to lie internally (Dzik & Martyshyn, 2015; thus, the external rugosity drapes over them rather than being integrated with them (Fig. 4B). A taxon like *Dickinsonia* is thus likely to have had a distinct upper and lower surface, separated by an internal cavity containing the channels; this internal cavity is likely to have been filled with ECM or some other inert material. Jenkins (1992), without illustration, argues that about 5% of *Dickinsonia* specimens show distortions consistent with the organism being a ‘somewhat under-stuffed sausage’, with the upper and lower surfaces sometimes rolling around the ‘stuffing’ to present atypical preservation. Flexibility in *Dickinsonia* is also indicated in transported specimens (Evans, Droser & Gehling, 2015). Although there have been persistent

claims in the literature that the upper and lower surfaces of *Dickinsonia* differ (e.g. Wade, 1972; Jenkins, 1992), this still remains unclear (for discussion, see Gehling *et al.*, 2005; Brasier & Antcliffe, 2008). The presence of both bilaterally symmetrical and asymmetrical *Dickinsonia* specimens may, however, imply that the two surfaces did differ (Wade, 1972; Gehling *et al.*, 2005). Perhaps a critical test of this view would be provided by the morphology of a taxon like *Pteridinium*, and whether or not its vanes are composed of one or two layers of tube-like structures (i.e. a direct comparison of the views of Grazhdankin & Seilacher, 2002 *versus* Jenkins, 1992); current imaging has not allowed definitive resolution of this issue (Meyer *et al.*, 2014a). Conversely, in at least *Stromatoveris* from the Chengjiang biota (Shu *et al.*, 2006), a Cambrian form potentially related to Ediacarans (Section III.2), the construction seems to be clear: a double wall surrounding a central cavity, with the walls themselves constructed of tubes.

If the above conjectures about morphological similarities between the circular and ‘bilateralomorph’ taxa are correct, then the probable body axis homology would be between the dorsal–ventral axis in forms like *Eoandromeda* or *Tribrachidium* and the anterior–posterior axis in *Spriggina* or *Dickinsonia*. In other words, the principal body axis for the former taxa would be in and out of the sediment surface, and along it

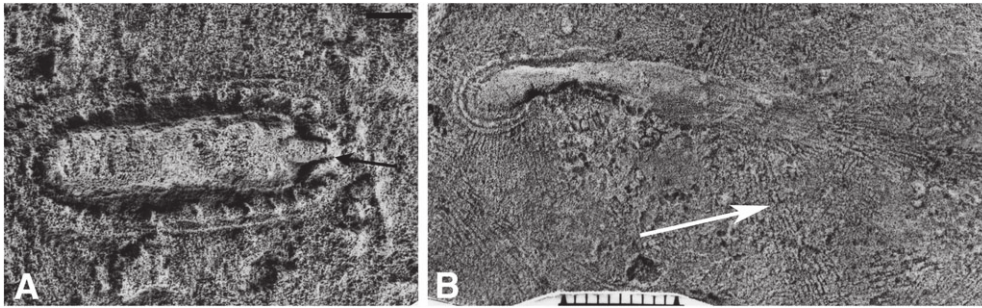


Fig. 5. *Kimberella quadrata* from the White Sea area in two different preservational aspects. (A) PIN4853/314 showing the ‘anterior’ introvert with a mushroom-shaped terminal body resembling *Parvancorina* (arrowed). (B) PIN 4853/334 in ‘frond-like’ position surrounded by the supposed feeding traces (ridges arrowed). Scale bar in (A), 2 mm; mm scale in (B). Photo credits: Andrej Ivantsov.

for the latter. It would suggest that forms such as *Spriggina* and *Dickinsonia* possessed rotational symmetry around their anterior–posterior axis (just as *Eoandromeda* has around its dorsal–ventral axis), which would explain the asymmetric ‘head’ regions in taxa such as *Ivovicia* and *Archaespinus fedonkini*. Very speculatively, if *Dickinsonia* had one surface divided in the middle and one surface not, then it may too possess a modified threefold symmetry.

(5) The problem of *Kimberella*

Perhaps the most discussed Ediacaran taxon is *Kimberella* (Fig. 5). We will look at this form in some detail as it is currently probably the only late Ediacaran fossil form that, although initially interpreted as a cnidarian (e.g. Glaessner & Daily, 1959), is now more or less universally accepted as a bilaterian metazoan, even by advocates of the Vendobionta. It also serves to illustrate the typical problems that are encountered in the interpretation of Ediacara-type fossils. Found in Australia and Russia, well-preserved material exhibits a wealth of detail not generally seen in other late Ediacaran macroscopic fossils, and it is also remarkable in being found with fan-shaped markings, apparently in direct continuation with the body fossils, that have been interpreted as trace fossils made by this organism (Fedonkin & Waggoner, 1997; Fedonkin, Simonetta & Ivantsov, 2007; Ivantsov, 2009, 2010, 2012, 2013). Specimens range from a few millimetres to 15 cm in length, and show considerable variation in morphology, some of which is taphonomic, but some of which may also reflect growth of the animal. Especially in material from Russia, dated to about 555 Ma, the fossils have been interpreted to show evidence for muscle fibres, mantle folds, a non-mineralized shell or dorsal cover, possibly with small sclerites, and a supposed head region. A neck-like anterior portion has been interpreted as a proboscis or introvert (Gehling *et al.*, 2005; Gehling, Runnegar & Droser, 2014), with possible teeth (Ivantsov, 2009, 2012), although the latter look similar to structures in the ‘posterior’ of the animal that have been interpreted as longitudinal muscle. In some specimens this structure is also remarkably similar to *Parvancorina* (see also Grazhdankin, 2014), raising the possibility that the latter is merely part of a larger organism.

It is probably not an overstatement to say that most of the above analyses of anatomical detail are open to discussion, and there remains little consensus on the placement of *Kimberella*. Erwin & Valentine (2013) considered it to be one of the few Ediacaran body fossils that require placement higher than the Cnidaria; most authors have, with varying degrees of confidence, considered it to be a mollusc or mollusc-like. Erwin *et al.* (2011) confidently assigned it to the crown metazoa, possibly as a mollusc, and, perhaps not very helpfully, erected the ‘clade’ Kimberellomorpha for *Kimberella* together with *Solza*, a form that Grazhdankin (2014) considered a likely taphonomic variety of *Kimberella*. This argument was based largely on an associated fan-shaped trace fossil claimed to show that *Kimberella* possessed a radula. Seilacher (1999) noted general similarities in the mode of preservation of *Kimberella* to that of experiments using modern molluscs such as the polyplacophoran *Katharina*. Although the animals in these experiments were placed in an orientation inverted relative to that of the preservation of *Kimberella*, there are intriguing general similarities. In some recent studies *Kimberella* has been accepted as a stem mollusc (Stöger *et al.*, 2013; Schrödl & Stöger, 2014; Vinther, 2015) although this seems to be based more on the authors’ argument that such animals should have existed at this time than on defining morphological features, or on the presence of very general bilaterian structures (Scheltema, 2014). Ivantsov (2009, 2012) instead suggested a more general placement in the ‘Trochozoa’. There have been few attempts to trace Cambrian relatives, although Caron *et al.* (2006) and Smith (2012), remarked on possible relationships with *Odontogriphus*, and Seilacher (1999) and Dzik (2011) suggested possible links to halwaxiids.

As mentioned above, *Kimberella* has been found associated with systems of variously developed paired ridges (Fig. 5B). Whereas *Kimberella* is typically preserved in negative relief on bed bases the associated sets consist of ridges on the bases of beds or grooves on bed tops. This difference in toponomy has been interpreted as the result of an animal raking microbial mats. Associated with these ridges and grooves are occasional sand pellets, which have been interpreted to have formed during the raking process, although their sometimes angular shape raises questions as to their origins (for example, they

may be casts of pyrite crystals). Although direct comparison has been made to scratches from molluscan radulae, most explicitly by Seilacher & Hagadorn (2000), their development in elongate fan-shaped forms and the considerable length of the scratches makes this unlikely (Ivantsov, 2009; Gehling *et al.*, 2014). If the organism stayed in one place and reached forward to form a series of parallel scratches (as in Gehling *et al.*, 2014) then it would have required a very long introvert in order to create the observed pattern, and this has not been seen. The sharpness of the ridges show that they were not formed in the mat but rather in sediment underlying the mat. The full length of the paired ridges therefore probably cannot be directly observed as they would only be preserved where they penetrate the mat. Following the finds of *Kimberella* body fossils in positions that suggest a direct association with the ridges, the most common interpretation is that they form a true association, but considerable uncertainty remains as to how the scratches were formed and by what type of device. The spatial association of fans and body fossils suggest a substantial amount of back and forth movement and with the supposed head region pointing away from the direction of motion (Ivantsov, 2009, 2012; Gehling *et al.*, 2014). Note that *Kimberella* body fossils found associated with supposed mucus trails also indicate movement in a direction contrary to that expected. It has been suggested that the ridges were formed by a radula, but a better comparison would probably be with the feeding organs of echiurans. Although not our preferred interpretation, there thus remain sufficient uncertainties in the interpretation of the fan-shaped ridges that a non-trace fossil interpretation should not be discarded (see also Brasier, 2009, p. 161).

As with all Ediacara-type fossils a critical question is whether to look for similarities or differences with living animals; taken to extremes these may lead to radically different conclusions. For example, there is a curious similarity of some elongate *Kimberella* to fronds (Fig. 5B). Continuing this comparison, the rounded terminal structures would be attachments and the radiating ridges would be interpreted as body fossil parts. General similarities can also be found between *Kimberella* and *Palaeophragmodictya spinosa* (Serezhnikova, 2009), with an outer zone and an inner zone with ‘hand’-like structures that in *Kimberella* have been interpreted as longitudinal muscle. The possibility that *Kimberella* is coelenterate grade should therefore not be excluded (see also Erwin, 2008). On a more general note, we find that the apparently unique sets of morphological, and possibly behavioural, traits in *Kimberella* mean that, although likely a metazoan, its placement remains problematic; it may be on the bilaterian stem group rather than within the stem group of any particular phylum – this is not incompatible with it retaining some coelenterate-grade features (e.g. Fig. 5B). One reason for suggesting that *Kimberella* is a stem bilaterian is the presence of the introvert (arrowed in Fig. 5A), the functional morphology of which may imply the use of hydrostatic pressure generated by an internalised body cavity such as a coelom; a typical bilaterian (and not ‘coelenterate’) feature.

(6) Ediacaran affinities

What then, are the Ediacarans? The evidence we review above strongly suggests that many fall into the stem regions around the base of the Animalia, Epitheliozoa and Eumetazoa. In particular, their three-dimensionality, sometimes contractile nature and presence of internal structures all militate strongly against the ‘Vendobionta’ theory of Seilacher (1992). We thus continue to think (see Budd & Jensen, 2000) that a strong *prima facie* case exists to consider them as falling into various fairly basal stem groups of large animal clades. An additional point in favour of their interpretation as stem-group metazoans is the fractal organisation of the early fronds such as *Rangea*; a large surface area (especially given the lack of any other feeding structures) may imply that these organisms fed, at least partly, *via* absorption of DOC from the sea water (e.g. Seilacher, 1984; Laflamme, Xiao & Kowalewski, 2009; Hoyal Cuthill & Conway Morris, 2014), a mode of feeding also known from sponges and choanoflagellates (Gold *et al.*, 1970; de Goeij *et al.*, 2008). Recent hydrodynamic modelling has highlighted the advantages to such osmotrophs of being raised above the sea floor (Ghisalberti *et al.*, 2014), an ecological selective force that may have led to the development of gastrulation-like mechanisms during development in order to generate an elevated structure. Rothman, Hayes & Summons (2003) suggested that the Proterozoic sea contained an enormous dissolved organic carbon reservoir, although this reconstruction has been recently challenged (Johnston *et al.*, 2012). The presence of frond-like Ediacarans in deep-water deposits such as at Mistaken Point (Narbonne, 2005) also suggests that they did not rely on photosynthesis for nutrition (i.e. that they were heterotrophs). Comparison with sponges suggests that if they were osmotrophs, a substantial symbiotic community of bacteria was necessary (Yahel *et al.*, 2003). Their appearance in the fossil record about 50 Ma after the end of the Marinoan glaciation at *c.* 630 Ma may thus truly record something close to the first stem-group animals, with the possible implication, given the continuity of the choanocyte, that they also filter-fed. The continuing absence of anything that could be convincingly considered to be a sponge (Antcliffe *et al.*, 2014) from the Precambrian (with the only exception perhaps provided by a demosponge-like taxon from the White Sea area that is figured, but not described, by Reitner & Wörheide, 2002) may imply that the crown-group sponges radiated as a monophyletic group in the Cambrian explosion like many other groups. Although this view continues to place the origin, not just of the bilaterians, but of crown-group animals, considerably later than molecular clock evidence suggests (Peterson *et al.*, 2004; Peterson & Butterfield, 2005; see also dos Reis *et al.*, 2015 for uncertainties in clock estimates of animal origins), we regard it as reasonable to state that there are no convincing crown-group animals in the fossil record until the first trace fossils appear at around 565 Ma or so (Liu *et al.*, 2014b).

As well as a likely stem-group animal placement for the early rangeomorphs, the various forms that cluster around

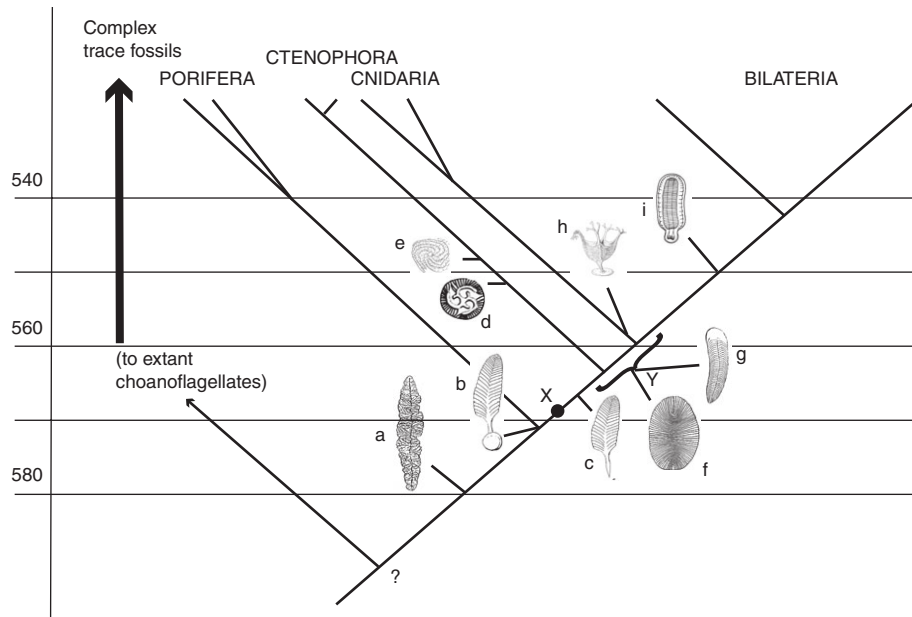


Fig. 6. An apoikozoan phylogeny (placozoans omitted) showing the possible positions of selected Ediacaran taxa. a, *Fractofusus*; b, *Charnia* ('fractal' form); c, *Charniodiscus* (non-fractal form); d, *Tribrachidium*; e, *Eoandromeda*; f, *Dickinsonia*; g, *Spriggina*; h, *Haootia*; i, *Kimberella*. X marks the transition from fractal (i.e. at least partly osmotrophic) to non-fractal fronds within the stem group of the Epitheliozoa; Y marks the 'coelenterate'-grade complex of taxa including *Dickinsonia*, *Spriggina* and related forms (see text for details). In the absence of both fossil and molecular clock data, the timing of the origin of crown-group Apoikozoa (marked '?') remains uncertain. Images adapted from Seilacher (1992), Xiao & Laflamme (2009), Zhu *et al.* (2008), Ivantsov (2012) and Liu *et al.* (2014a).

Dickinsonia to *Eoandromeda* seem likely to consist of two body layers separated by an inner substance (ECM?) within which are internal branching canals. This would be a classical diploblastic organisation; this view of these taxa is reinforced by the ctenophore-like features of *Eoandromeda*. This is not to say that all these taxa are stem-group ctenophores (or, indeed, cnidarians). Nevertheless, the apparent presence of some sort of internal cavity is consonant with, and indeed required by, these organisms lying within the 'coelenterate' grade as marked on Fig. 1. It is thus possible that ctenophores living today have retained some profound plesiomorphies that were present along the various metazoan stem-groups. Overall, we regard this evidence as strongly supporting a placement within a 'coelenterate' grade (see comments by Zhang & Reitner, 2006, who come to very similar conclusions).

Many of the macroscopic Ediacaran fossils of possible animal affinity, although not united into a monophyletic clade, may thus be considered to be a plesiomorphic collection of stem-group animals that must necessarily include stem-group sponges and ctenophores and, after the stepwise appearance of taxa such as the (unknown) makers of early trace fossils, and the first skeletonised taxa such as *Cloudina* (Grant, 1990), stem-group cnidarians and bilaterians. These rather tentative hints allow a more general view to be taken of Ediacaran affinities: the rangeomorphs, based on general considerations such as their modularity and inferred feeding modes, are likely to be very basal or stem-group metazoans, and the *Eoandromeda* group are total-group ctenophores. Given that early Ediacaran forms usually have

divided ('fractal') branches, and ones that emerge later do not, then perhaps some forms may represent a fractal to non-fractal transition (see also Brasier & Antcliffe, 2004; Brasier *et al.*, 2012). This allows the stems of metazoan taxa to be tentatively populated by various Ediacarans (Fig. 6). It should be noted that in this view, crown-group cnidarians, bilaterians and sponges did not emerge until very close to, or potentially even after, the beginning of the Cambrian.

Given that the majority or all of these forms appear to be benthic, the question arises: how were they feeding? The presence of a set of branching internal cavities attached to a central tube strongly suggests that an opening to the outside must exist, even if evidence for it is slim (e.g. Jenkins, 1992; Dzik & Ivantsov, 2002; see comments in Gehling *et al.*, 2005). The apparent absence of a mouth in these forms has been taken as strong evidence that they are not animals. However, this point is not unsurmountable. The mouth may be small or lie on a margin (as suggested by our symmetry homologies in Section II.4) where it would be difficult to detect. To take extant benthic ctenophores as a useful analogy, they largely feed with long and feathery retractable tentacles that gather food from the water column (Rankin, 1956). Although these would be unlikely to be preserved, there are perhaps suggestions of such structures in the type specimen of *Iovicia rugulosa* (Fig. 2A), which displays slender thread-like objects around the 'posterior' of the organism. Another possibility is provided by the slight, but perhaps intriguing similarity of the supposed 'pharynx' region of *Dickinsonia* to the terminal structure of *Kimberella* (Figs 4E and 5A), suggesting that

Dickinsonia perhaps also possessed an introvert-like structure. Its position at the base of the so-called ‘spatulate segment’ of Brasier & Antcliffe (2008), which is a region of apparent structural weakness, may be of significance. However, we wish to stress that there is no particular reason to think of the Ediacaran taxa as being direct ancestors of the modern (and derived, see Simion *et al.*, 2015) benthic ctenophores.

(7) Major transitions in early animal body plans

These early organisms force on us some hard problems, including how presumably osmotrophic and/or filter-feeding basal members of the clade evolved into the predatory, suspension or deposit feeders that characterise the metazoans. Given our profound ignorance of how this happened, the challenging possibility that large shifts in feeding and other ecological strategies took place without substantial reorganisation of the body plan must be taken seriously. Indeed, if our view of the Ediacarans is broadly correct, then the interesting corollary is that the various stem groups of large metazoan taxa were rather conservative morphologically; perhaps this makes sense in a scenario of very rapid adaption to new ecological niches. This would explain the (relative) morphological similarity of the Ediacarans and their proposed highly paraphyletic relationships relative to modern clades. In this view, the enormous ecological opportunities that were opening up to multicellular heterotrophs in the Ediacaran implies that very rapid ecological shifts took place within a rather homogeneous assemblage, and that only later did distinctive ‘body plan’ adaptations sequentially start to appear.

The theoretical problems involved in moving between the major grades of animal organisation have led to several attempts at circumventing the issues, usually by ‘resetting’ morphology *via* heterochrony. Thus, a typical view would be that the eumetazoans are derived from the larva of a sponge-like organism (Nielsen, 2008), or that the bilaterians are derived from the larva of a cnidarian. A novel approach was that of Dewel (2000) who, taking seriously the possibility of adult body plan evolution, proposed that modularity in early animals gave rise to coloniality which then led to a further round of integration to derive a complex basal bilaterian from a colonial pennatulacean-like ancestor (see also Beklemishev, 1964). If the transformations outlined here are broadly correct, then although the details (discussed in Dewel, 2000) of the evolution of organ systems such as the through gut, excretory structures such as proto and metanephridia, circulatory system, etc., remain obscure, there seems no reason to invoke dramatic heterochronic transformations, even if heterochronic changes may be involved at some level.

III. THE FATE OF THE EDIACARANS AND THE RISE OF THE BILATERIANS

Before the modern dating era it was widely considered that the Ediacaran biota considerably pre-dated the Cambrian

(Laflamme *et al.*, 2013; MacGabhann, 2014), and even after redating placed the two biotas in close temporal proximity, there has been a tendency to regard them as being separated by a mass extinction (e.g. Amthor *et al.*, 2003; Narbonne, 2005; Darroch *et al.*, 2015). Given that bilaterian animals, so characteristic of Cambrian biotas, are inferred to have existed in some form since at least the latest Ediacaran (through the trace fossil record), a model of biotic replacement that was perhaps mediated by a mass extinction has often seemed attractive (e.g. Seilacher, 1984; Laflamme *et al.*, 2013). Perhaps this assumption is influenced by the subordinate mammals supposedly only being free to radiate into newly vacated niches after extinction of the dinosaurs at the end of the Cretaceous. The extinction of the Ediacarans has also been considered as a form of trophic amensalism, with the newly evolving sediment-churning bilaterians radically changing the substrate to exclude them (Laflamme *et al.*, 2013). One final possibility, favoured by Laflamme *et al.* (2013) is that the metazoans were simply more efficient at occupying benthic space, and thus indirectly outcompeted the Ediacarans. Several lines of evidence suggest that these simple models may not fully capture the complexity of bilaterian–Ediacaran interactions, both ecologically and (thus) evolutionarily. We explore these issues first by considering bilaterian ecology in the Ediacaran, then Ediacaran organism survival into the Phanerozoic.

(1) Early animal bioturbation

Animals burrow for a range of reasons. Permanent dwelling structures may provide protection against predation but also from adverse environmental conditions. In particular vertical permanent burrows are constructed by filter-feeders feeding in the water column or on a water current diverted to enter the burrow. Deposit feeding covers a range of behaviour in which the organism extracts nutrients from the sediment. Movement within the endobenthos, such as in echinurans, removes sediment with an effect that depends on the size of the producer and its activity. Vertical displacement of sediment is particularly effected by conveyor-belt deposit feeders, including many polychaetes, that feed within the sediment and defecate on the sediment surface. Particular influence on the sediment geochemical profile comes from bioirrigators, that actively pump water through a permanent burrow system. This is only a selection of the various ways in which animals can use sediment. The important point we wish to emphasise is that many of these activities, such as effective bio-irrigation and conveyor-belt feeding, are much more effective when carried out by an animal with well-developed (and differentiated) limbs, and therefore were presumably not present until well into the Cambrian or even later. The situation here is similar to that of the role that filtering animals may have had on the transparency of the water column; available evidence suggests an appearance that post-dates the event that they have been suggested to have been involved in (see Butterfield, 2009; Xiao, 2014).

The impact of bioturbation in deep time has recently received increasing interest, in particular in relationship

to the Ediacaran–Cambrian transition (McIlroy & Logan, 1999). It is well known that bioturbation significantly modifies the topography and geochemical profile of the sea floor. Experiments have shown that in the absence of bioturbation microbial mats will develop on the sea floor (e.g. Fenchel, 1998). It is thus reasonable to suggest that such mats would have been well developed on the sea floor prior to the advent of bioturbation (Seilacher & Pflüger, 1994; Schieber *et al.*, 2007). This is supported by the prevalence in Precambrian siliciclastic sediments of sedimentary structures that have been interpreted as being induced by or related to such biomats. The suggestion has been made that the early evolution of animals would have been more or less intimately related to these microbial mats either as anchoring substrates or as a food source (e.g. Stanley, 1973; Gingras *et al.*, 2011; Meyer *et al.*, 2014b). Simple essentially horizontal trace fossils created a short distance below the sediment–water interface have been interpreted as formed by animals feeding on buried mats (Fig. 7; Seilacher, 1999; Gehling, 1999). Both the lack of significant bioturbation and the sealing effect of the mats, made especially effective by the production of large amounts of mucilage by cyanobacteria (Stal, 2012, p. 115) would have led to much sharper geochemical gradients in the sea floor compared to those in most modern sea floors. Such gradients expand, and become spatially more complex, with the introduction of bioturbation, in turn making deeper sediments of greater interest to deposit-feeders. This change from a ‘mat-ground’ to a ‘mix-ground’ has been referred to as an agronomic revolution (Seilacher & Pflüger, 1994), and has been seen as an early example of ecosystem engineering (e.g. Meysman, Middelburg & Heip, 2006; Marenco & Bottjer, 2007). Studies have considered both direct and indirect negative effects of the rise of bioturbation on fossil preservation (Brasier, Antcliff & Callow, 2011), and the global effect of bioturbation on oxygen and phosphorous cycles (Boyle *et al.*, 2014). Although there is a continuous record of discrete trace fossils from at least 560 Ma (Fig. 7), evidence for effective sediment mixing only appears well into the lower Cambrian strata (e.g. Mángano & Buatois, 2014). The only well-documented possible example of extensive latest Ediacaran sediment mixing has been reported from the Khatyspyt Formation of Siberia (Rogov *et al.*, 2012), but remains under discussion as an alternative interpretation of body fossils must be considered (Brasier *et al.*, 2013; Gámez Vintaned & Zhuravlev, 2013; Rogov *et al.*, 2013a,b). Overall we think it is important to repeat our conviction (Budd & Jensen, 2000, 2003) that the radical difference between typical Ediacaran and Cambrian trace fossils, both in size and complexity (see Fig. 7), is informative about bilaterian evolution, and that this pattern is irreconcilable with deep divergence times for the major bilaterian clades.

(2) Cambrian Ediacarans?

The relationship between bioturbation and the Ediacarans may not be simple. Sparse trace fossils are common in Ediacaran assemblages, and important new material from

the Shibantan biota (Chen *et al.*, 2014) shows that Ediacarans could co-exist with prominent horizontal burrowing. Note that many extant metazoans that are intolerant of high levels of bioturbation (Rhoads & Young, 1970) simply live in the many facies where bioturbation is limited. The fossil record of Ediacaran biotas, although very sparse (like that of all poorly preservable taxa), is potentially quite widespread in the Cambrian (Figs 8 and 9). Taxa purportedly from this assemblage have been reported from rocks of Cambrian age on various continents (e.g. Conway Morris, 1993; Jensen, Gehling & Droser, 1998; Crimes & McIlroy, 1999; Hagadorn, Fedo & Waggoner, 2000; Zhang & Babcock, 2001; Shu *et al.*, 2006; Babcock & Ciampaglio, 2007). In addition to these reports from south China, North America, Baltica and Australia, *Swartpuntia* and *Pteridinium* in Namibia range above ash-beds with dates within the error of that currently accepted for the base of the Cambrian, *c.* 542 Ma (Narbonne, Saylor & Grotzinger, 1997; Schmitz, 2012).

The examples from California consist of poorly preserved but relatively convincing *Swartpuntia*-like taxa from rocks that are above those containing the first trilobites in the region, and are likely to be considerably younger than 520 Ma (Hagadorn & Waggoner, 2000; Hagadorn *et al.*, 2000). Similarly convincing taxa, especially *Thaumaptilon*, which has similarities to *Charniodiscus* from e.g. the White Sea area, northern Russia, are known from the Middle Cambrian Burgess Shale (Conway Morris, 1993), dated to about 506 Ma. *Thaumaptilon* is problematic, because its original description suggested that the small dark spots scattered around its surface represent the remains of zooids, implying a colonial and thus cnidarian affinity similar to a pennatulacean. However, the scattered but closely packed nature of these dark spots (Fig. 8B) is not similar to the distribution of zooids in modern pennatulaceans, and there seems no particular reason to assume a relationship. These structures might represent eggs, for example. A candidate pennatulacean is known from the Chengjiang fauna (see supplementary information in Shu *et al.*, 2006), and does not appear to be particularly similar to *Thaumaptilon*.

The Cambrian survivors, some of which are admittedly controversial (for a more skeptical view, see Laflamme *et al.*, 2013), represent more than just curiosities. Whilst rare as fossils, the fact that they are reported from several continents, and over a long period of Cambrian time, suggests that they were not insignificant components of the Cambrian biota. Given the inevitable biases of the fossil record (e.g. Valentine *et al.*, 2006) it should be noted that geographically and ecologically widespread taxa are more likely to leave evidence in the fossil record. Thus even though they are rare in Cambrian fossil assemblages, Ediacara-style organisms may have been relatively common in the Cambrian period. Indeed, the length of time they seem to have persisted in Cambrian sediments (*c.* 25 Ma) is not dissimilar to the *c.* 37 Ma for which they are known from the Ediacaran, and there is no reason to assume that the Burgess Shale examples are the last in the Phanerozoic (see Marshall, 1990 for a discussion of the range extension of taxa). Recent discoveries

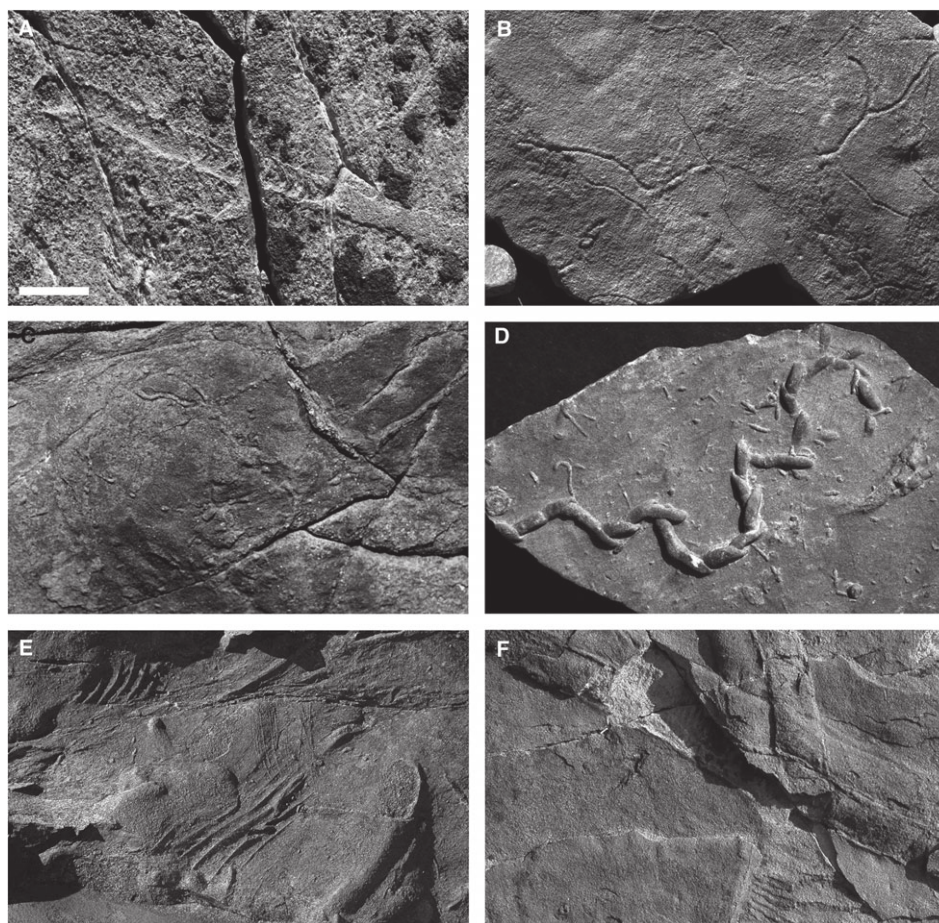


Fig. 7. Typical Ediacaran (A–C) and lower Cambrian (D–F) trace fossils, all to the same scale. (A) Trace fossils from the Mistaken Point Formation, Newfoundland, reported by Liu *et al.* (2010, 2014b), representing some of the oldest credible evidence for metazoan mobility. (B) Upper sandstone bedding surface with typical examples of late Ediacaran trace fossils. Nilpena, Ediacara Member, South Australia. (C) Lower bedding surface with small *Planolites*-type trace fossils, preserved as short burrows and vertical and inclined knobs. Also seen are sand-filled shrinkage cracks. Member 1 of Chapel Island Formation, Burin Peninsula, Newfoundland. (D) *Treptichnus pedum* preserved in positive hyporelief. Mickwitzia sandstone member, Västergötland, Sweden. Note small burrows of a scale and development similar to the traces in (C). (E) *Monomorphichnus* isp. Member 2 of the Chapel Island Formation, Burin Peninsula, Newfoundland. This type of trace is generally attributed to arthropod limbs. (F) *Plagiogmus arcuatus* from the Arumbera sandstone, central Australia, showing the complex structure of this type of trace. Scale bar in (A) applies to all parts, 20 mm. Photo credits: (A) Alex Liu, (B–E) S. J.

in the Ordovician Fezouata Biota seem to indicate that taxa classically thought to be Cambrian must have persisted much later into the Palaeozoic (e.g. Van Roy, Daley & Briggs, 2015). If one accepts six separate occurrences of complex Ediacaran survivors in the Cambrian (Namibia, Australia, two from California, Chengjiang and Burgess Shale; Fig. 10) then a simple calculation places the 95% upwards range extension at about 475 Ma, i.e. well into the Ordovician. Furthermore, if Boucot (1983) is correct, then apparent stasis in the morphology of these organisms may also indicate ecological abundance. Finally, another point in favour of the Cambrian examples being true Ediacaran survivors is that they are all from morphogroups known from the ‘Kotlinian’ upper Ediacaran assemblages (Grazhdankin, 2014), suggesting a Precambrian decline in Ediacaran diversity. Conversely, it should be noted that the supposed

bilaterians such as *Kimberella* are known from the middle, ‘Belomorian’ stage and apparently disappear before the end of the Ediacaran (Xiao & Laflamme, 2009; Grazhdankin, 2014), a stratigraphic discontinuity that questions their supposed continuity with Cambrian bilaterians, unless a significant reduction in Ediacara-style preservation is invoked to have occurred well before the base of the Cambrian, perhaps because of an increase in bioturbation. Buatois *et al.* (2014), however, reported matground-based ecology to have persisted well into the Cambrian from which they concluded the decline of Ediacarans to be a real event and not an artefact of preservation. Even in the absence of body fossils the presence of these organisms could potentially be evidenced from tool marks (passive scraping of the body along the sediment) as they were carried by currents. Both *Pteridinium* and *Swartpuntia* are known to produce tool marks in

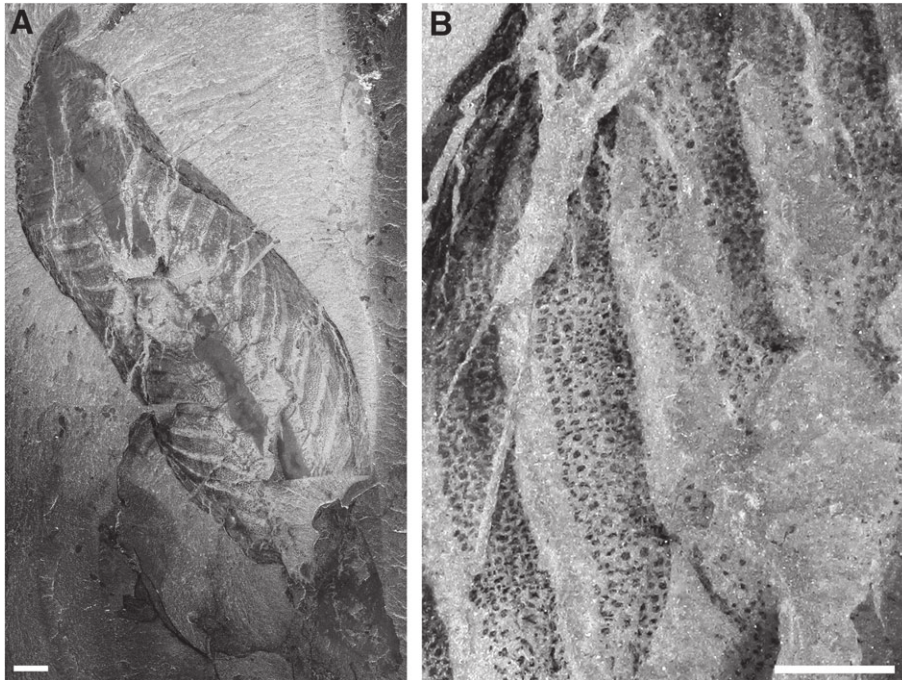


Fig. 8. (A) *Thaumaptilon walcotti* (USNM 468028) from the middle Cambrian Burgess Shale of Canada, showing its general resemblance to some *Chamiodiscus*. (B) *T. walcotti* enlargement showing the irregular dark spots considered to represent zoids by Conway Morris (1993). Here they may be seen to lie within distinct close-packed cells, perhaps with some resemblance to eggs. Scale bars, 10 mm. Smithsonian Institution (NMNH). Photograph: Jean-Bernard Caron.

Ediacaran age sediments. Examination of early Phanerozoic tool marks (and those of *Monomorhichnus* – Fig. 7E) might potentially add evidence for the presence of Ediacara-type organisms in this period.

Not only did Ediacara-type biotas apparently survive until well into the Cambrian or beyond, but the bilaterians themselves were evident from about 560 Ma onwards in the form of trace fossils (Martin *et al.*, 2000: for arguments that these are bilaterian in origin, see Budd, 2015). Earlier trace fossils have been documented from the *c.* 565 Ma Mistaken Point biota (Fig. 7A; Liu *et al.*, 2010, 2014b) but these are too simple to be confidently assigned to bilaterians, and could have been made by a cnidarian or similar (Liu *et al.*, 2010). Unlike Phanerozoic trace fossils that are typically found in environments that do not preserve body fossils, the Ediacaran traces are found in beds that also contain Ediacara-type biota, even if this relationship is sometimes obscured by differential preservation (see e.g. comments about deeper-water ‘Fermeuse-style preservation’ in Narbonne, 2005). Although the exact relationship between Ediacaran body and trace fossil assemblages has yet to be explored (for example, in terms of bed-by-bed variation) it seems reasonable to conclude that the early mobile bilaterians were members of communities including the largely sessile Ediacaran-type biota (e.g. Gehling & Droser, 2013; Xiao *et al.*, 2013; Chen *et al.*, 2014; see also fig. 184 of Gehling & Vickers-Rich, 2007), and an often-neglected algal component (Xiao *et al.*, 2013). This bilaterian/Ediacaran relationship apparently persisted for at least 50 Ma.

(3) Savannah environments as an analogue for the Ediacaran sea floor

We here suggest an alternative linkage between Ediacaran and Cambrian diversity that is consistent with their long co-existence. This linkage reflects the disturbance and regionalisation of the benthic habitat by Ediacara-aspect taxa that created considerable spatial heterogeneity in resources (including organic carbon); it was this increase in β -diversity that was the proximal cause of the subsequent radiation of bilaterians. We call this the ‘savannah’ hypothesis because it compares Ediacaran environments to highly structured modern savannah environments (Fig. 10) in which trees are scattered across plains in proximity to other habitats such as hills. This environment provides a spatially highly heterogeneous resource distribution. Indeed, as well as the high diversity of ungulates supported by the modern savannah, a well-known hypothesis of human evolution suggests that bipedality evolved as a response to movement between the scattered resource hotspots (Rodman & McHenry, 1980; Isbell & Young, 1996). In savannah environments, soil organic content (SOC) appears to be correlated both with the total above-ground carbon content (Alam, Starr & Clark, 2013) and at the micro-level with the distance from individual trees (Weltzin & Coughenour, 1990).

Arguments that large sessile organisms can provide spatial heterogeneity in terrestrial environments can also be applied to the benthic environments of the marine realm. Large

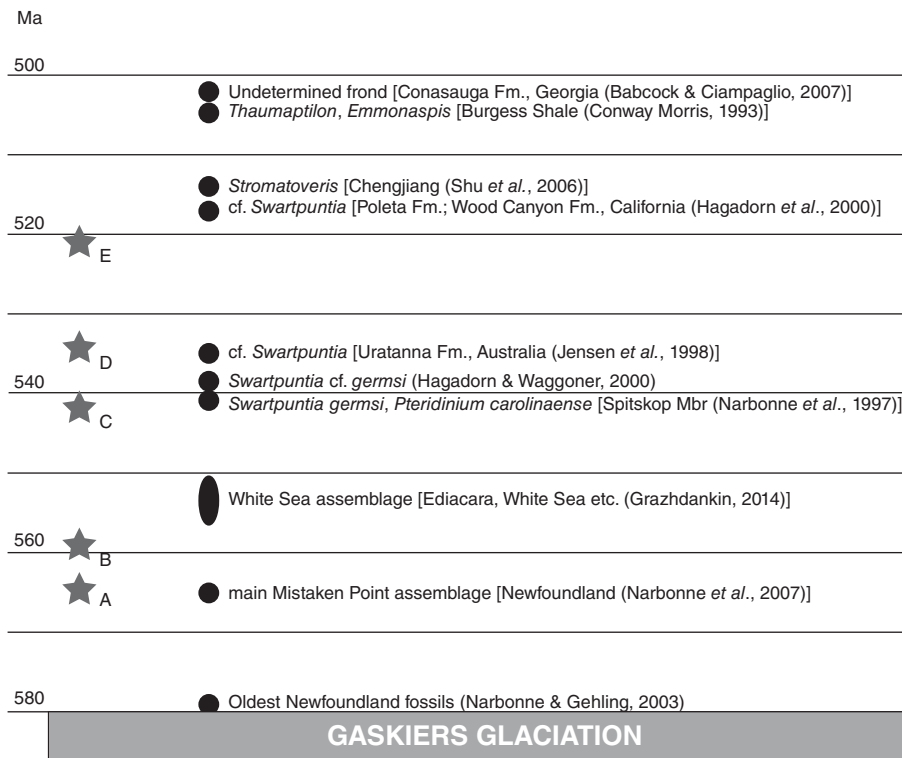


Fig. 9. Putative 'Ediacaran' occurrences in the Ediacaran and Cambrian. Ediacaran-Cambrian boundary is at *c.* 542 Ma. Evolutionary landmarks are marked by stars. (A) Oldest probable metazoan trace fossils (Liu *et al.*, 2010); (B) oldest simple (total-group bilaterian) trace fossils (Martin *et al.*, 2000); (C) oldest *Treptichnus pedum* (complex three-dimensional trace fossils); (D) oldest clear arthropod traces (*Monomorphichus*-type traces extend a little lower); (E) oldest trilobites.

stationary organisms in the deep sea such as xenophyophores (Levin *et al.*, 1986; Levin, 1994), which were potentially present in the Ediacaran (Seilacher, Grazhdankin & Legouta, 2003; see Antcliffe, Gooday & Brasier, 2011 who conclude that *Palaeopascichnus* may have been a large protist if not a xenophyophore), generate concentrations of nutrients in the surrounding sediment as well as providing diversity hotspots, partly because of the increased vertical space they make available to at least the epifauna and probably the infauna as well. Jumars (1976) provided arguments that biodiversity can be affected by environmental heterogeneity of less than 10 cm, i.e. a scale consistent with the heterogeneity provided by individual organisms (see also Widdicombe & Austen, 2005 who come to similar conclusions). This is particularly relevant to Ediacaran communities, which despite many similarities to modern communities in terms of composition have been suggested to be highly homogeneous at the large scale (Clapham, Narbonne & Gehling, 2003), at least at Mistaken Point. The increasing recognition that many fossils in this setting represent, not a 'Pompeii'-style sudden obliteration of a pristine community, but rather to some extent represent large numbers of organisms in various states of decay (Liu *et al.*, 2011) suggests that dead organisms would also contribute to resource heterogeneity [*cf.* remarks in Liu *et al.* (2015) on the utility of dead Ediacarans for providing resources; and Laflamme, Schiffbauer & Narbonne

(2011) and Wilby, Carney & Howe (2011) for alternative interpretations as microbial colonies and taphonomic loading structures]. Just as trees in the savannah provide shelter for herbs, which has a positive feedback on SOC production, increased diversity in the vicinity of sessile organisms may increase sediment organic carbon content around them.

Although the effect of small-scale heterogeneity on community dynamics has typically been excluded in experimental approaches (e.g. Raffaelli *et al.*, 2003), there is a growing understanding that it may be of considerable importance in controlling faunal dynamics and diversity. In particular, the effect of heterogeneity on movement of the benthos was studied by Levinton & Kelaher (2004) and Bulling *et al.* (2008), with the hypothesis being that mobile benthic organisms should move towards resource-rich patches, deplete them, and then move away. However, experimental data shows mixed responses by the benthos. Deposit feeders such as *Hediste diversicolor* and *Hydrobia ulvae* tend to move towards resource-rich areas, whereas the amphipod *Corophium volutator* moved away. Such movements may be dependent on the different ecologies of these organisms, but another important factor is the modification of the environment caused by resource-rich patches. In particular, the decay of organic matter creates areas of hypoxia that organisms tolerate differently (Olafsson, 1992; Norkko, 1998). The ability to withstand hypoxia brings at least two



Fig. 10. A typical heterogeneous savannah environment in the Serengeti, Tanzania. Note diversity-generating heterogeneity in the landscape caused by topography, type and distribution of vegetation, and animal behaviour (e.g. the termite mound, centre, often secondarily inhabited by mammals). All of these aspects have analogues in the Ediacaran environment. Photo: G. E. B.

benefits: it allows decaying organic matter to be utilised as food, and also as a refuge against less hypoxia-tolerant predators (Norkko & Bonsdorff, 1996; Norkko, 1998).

In modern environments, habitat disturbance and heterogeneity are also greatly influenced by bioturbation (e.g. Lohrer, Thrush & Gibbs, 2004; Meysman *et al.*, 2006). However, in the Ediacaran period, before large-scale bioturbation had commenced, it seems likely that the effects of individual sessile organisms – living and dead – may have been the major source of biologically mediated habitat heterogeneity [see also Plotnick, Dornbos & Chen (2010) and Mángano *et al.* (2012) who discuss spatial heterogeneity in the context of the Cambrian, and Liu *et al.* (2015) who discuss Ediacaran examples]. This largely static early period of Ediacara-style taxa with no bioturbation would have led to a relative lack of horizontal organic carbon transfer within the sediment, which today is largely a result of bioturbation (Wheatcroft *et al.*, 1990; Wheatcroft, 1991). As a result, organic carbon sinks such as early Ediacaran taxa, either during their life or death, would have been particularly prone to creating organic carbon hotspots in the sediment. The relative lack of horizontal transfer would thus perhaps have tended to make the death of Ediacarans somewhat akin to modern whale falls, where up to 2000 years of organic carbon export can be sedimented at once and concentrated in a small area (Smith & Baco, 2003; see Mángano *et al.*, 2012). Ediacaran macroalgae would also have been important in this context (Wang *et al.*, 2014), and a better understanding of their spatial distribution with respect to Ediacara-type organisms would be of interest. Finally, the residence time of organic carbon in different environments would have enhanced this effect in certain environments. For example, organic carbon is stabilised in fine-grain sediments such as clays, but destabilised in

environments such as high-energy sandy deposits (e.g. Kennedy, Pevear & Hill, 2002). Given the same rate of organic carbon supply from Ediacaran taxa in each, it follows that the ‘SOC’ concentration gradient would be higher in sandy environments than in muddy ones, because ‘SOC’ would be degraded faster in the former environments. Note also that organic carbon in general is likely to have degraded faster in Ediacaran sediments than it does today, because of the lack of refractory organic carbon derived from terrestrial sources.

As noted by Butterfield (1997), the problem of organic carbon supply in the Ediacaran was probably not one of lack as such but of concentration. Without the clumping effect generated by the modern mesozooplankton, organic carbon export to the sea floor would have been highly homogeneous, which would have made obtaining nutrition highly problematic. Its export to sediments may have been further limited by large-scale microbial mat communities effectively ‘sealing off’ sediments from the sea water above them. Organic carbon content in sediments may thus largely have been produced from microbial mats themselves, either during their decay, or by direct organic carbon production *via* fixation of DOC in sea water. Rather than clumping being provided by cryptic mesoplankton (e.g. Logan *et al.*, 1995), we suggest that this concentration of resources largely took place within the sediment as the result of the growth and death of large sessile Ediacara-style taxa (Fig. 11). This resource concentration may have made burrowing energetically viable, just as resource concentration on the savannah may have facilitated bipedality in early humans. A transition from early bilaterians living largely on the surface and feeding off mats that surrounded the Ediacara-style biota to true burrowing may have been facilitated by partial burial of such mats, with their indigenous fauna continuing to feed on them even when below the surface.

The remnants of this early ecological framework may have persisted well into the Cambrian, where, for example, beds containing both trilobites and Ediacara-style taxa seem to be known from both Laurentia (Conway Morris, 1993; Hagadorn *et al.*, 2000) and South China (Shu *et al.*, 2006). As Cambrian taxa diversified, they would have rapidly ceased reliance on Ediacara-style taxa to provide spatial heterogeneity, and perhaps this may have been one feature in the ultimate demise of the Ediacara-style taxa. When this happened remains quite unclear.

Given the above hypothesis, it would be interesting to see if any direct relationships can be detected between Ediacaran body and trace fossils, either positive or negative. In principle, theoretical modelling suggests that trace fossil production should differ between resource heterogeneous and homogeneous environments (Kitchell, 1979). In addition, optimal foraging theory assumes that organisms act in order to (i) maximise energy intake; (ii) spend optimal time within food patches; and (iii) move in an optimal way from one patch to the next (e.g. Senft *et al.*, 1987). It would be of interest to see if trace fossil relationships with fossils of known living and known dead organisms

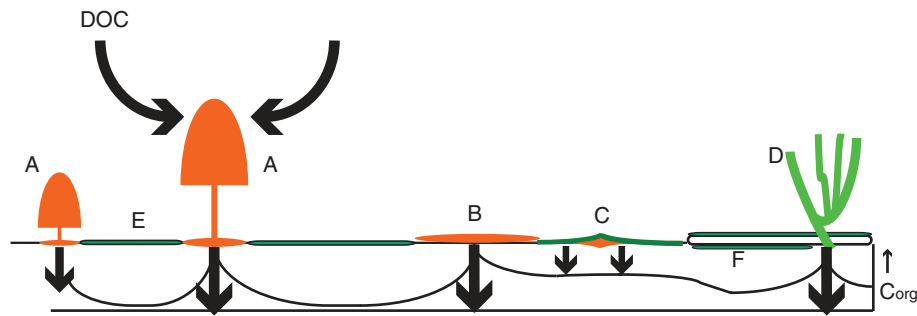


Fig. 11. Schematic view of carbon resources and flow in the ‘Ediacaran savannah’, showing assimilation of dissolved or particulate organic matter into sessile (A), prone (B) and decaying (C) Ediacarans and algae (D), with living (E) and buried (F) cyanobacterial mats. The graph below shows qualitative buried organic carbon (C_{org}) distribution; similar arguments would apply to sea-floor C_{org} distribution. Note overgrowth of decaying Ediacaran to produce ‘death mask’ preservation (e.g. Gehling *et al.*, 2005). DOC, dissolved organic carbon.

differed in Ediacaran communities, for example. As far as we know, this relationship has not been explored, although some analogous evidence exists from the Cambrian. For example, in the Sirius Passet biota, trace fossils seem to be concentrated around and even associated with body fossils [Mángano *et al.* (2012), an association first noted and figured by Budd (2011)]. Arguments advanced by Plotnick *et al.* (2010) and Mángano *et al.* (2012) that carcasses in the Cambrian supplied concentrations of nutrients should in principle also be applicable to Ediacaran assemblages. On the other hand, it may be that taphonomic barriers exist to the preservation of this sort of interaction as the trace fossils and body fossils may be preserved at different levels (see e.g. Narbonne, 2005 for remarks about the ‘Fermeuse’ style of preservation in Newfoundland). Finally, the distribution of the Ediacaran taxa themselves may have been influenced by the concentration of organic carbon resources around individual taxa, and this may help explain the distinctive (reproductively mediated?) distribution of taxa such as *Fractofusus* that has recently been reported (Mitchell *et al.*, 2015).

IV. DISCUSSION

Although our knowledge of the Ediacaran organisms remains frustratingly limited, many indicators point towards their placement within the animals. These indicators include: (i) appearance in the fossil record just before bilaterians, and the complete absence of other fossils that might be assigned to more basal clades; (ii) the presence of diploblastic features (which phylogenetic reconstruction suggests should be present in deep internal branches in the metazoans) such as a double body layer with an internal branching cavity that must lie within the body itself, likely filled with an ECM-like substance; (iii) morphological linkages of at least one (*Eoandromeda*) to extant ctenophores, together with potential links between it and other Ediacaran taxa; (iv) the absence of obvious apomorphies uniting these taxa within any crown-group phyla. In addition, it should be noted that the earliest assemblages are dominated entirely by

rangeomorph forms such as *Fractofusus* and *Bradgatia*. Their morphology is consistent with an at least partly osmotrophic mode of feeding, suggesting placement within the animals (i.e. they are heterotrophs), but falling outside the Epitheliozoa (i.e. below the node subtending Ctenophora and Eumetazoa). The limited stratigraphic evidence is consistent with the earliest Ediacarans belonging to very deep clades within the Metazoa, and later ones being members of the Epitheliozoa. These two basic types of Ediacarans could in principle be linked by a transition between fractal and non-fractal forms; if this link can be maintained, then the Ediacaran assemblages would, remarkably, provide information about one of the most important, but hitherto highly obscure, transitions in animal evolution. Thus, although the affinities of Ediacarans have acquired an almost mystical status, we believe that the most obvious explanation for their affinities – that they represent the early stages of animal evolution – is the one that is also the best supported. We do not believe that any other model of affinities of any of the Ediacarans can account so well for their temporal and environmental distribution, overall morphology or apparent patterns of relationship (indeed, no other model even attempts to do so). Even more so than for the taxa from the Burgess Shale-type biotas (Budd & Jensen, 2000), interpretation of the Ediacaran taxa has been hampered by a failure rigorously to apply stem- and crown-group concepts.

The relationship between the taxa known from the Ediacaran assemblages and the later radiations that constitute the Cambrian explosion has largely been considered to be negative, with Ediacarans occupying niches were emptied before the bilaterians could radiate. Here we propose a much more positive relationship between these two sets of taxa, that the Ediacarans actually provided a highly structured and resource-heterogeneous environment that was an essential framework within which the bilaterians could radiate (Fig. 11). Although limited ecological diversification might have been possible by simply feeding off the mats, early bilaterians may have been limited by their essential inability to access material lost to the sediment by death, excretion, etc., until they managed to solve the problem

of sub-surface feeding by burrowing, at least shallowly. Furthermore, homogeneous microbial mats may have provided only limited possibilities for supporting increased benthic diversity of evolving bilaterians because of their inability to provide habitat heterogeneity. Given the high energy demands of burrowing, such a lifestyle may not have been possible without resource concentration as outlined here. However, once this process started, it would have led to an ecological cascade, with innovations such as infaunal predation becoming possible, in turn triggering higher levels of burrowing, and eventually leading to the slow transformation of the environment in the so-called ‘Cambrian substrate revolution’ (Bottjer, Hagadorn & Dornbos, 2000). However, this process may have been slowed by the continued dependence of the early bilaterians on Ediacaran-type taxa for resource generation and habitat heterogeneity until well into the Cambrian, when sponge and other sessile communities eventually broke this ecological dependency. The archaic Ediacaran-style biota would then have switched from being enabling to being threatened by the radiating bilaterians, and their niches broadly replaced by new sessile organisms such as sponges and various tube dwellers that are characteristic of the latest Ediacaran and earliest Cambrian faunas. Although we have focused herein on the influence of the largely static Ediacaran taxa on structuring early bilaterian evolution, it would be inevitable that the Ediacaran communities themselves would respond to the diversification of the bilaterians. It would thus be interesting to see if any restructuring of Ediacaran communities took place towards the end of the period, when trace fossils start to diversify. Finally, it is worth noting that such structuring of metazoan communities by pre-existing and co-evolving organisms seems to have persisted into the Cambrian in the guise of microbial reefs facilitating metazoan diversity (e.g. Riding, 2011).

Previous ecological accounts of the rise of the bilaterians (e.g. Stanley, 1973; Gingras *et al.*, 2011) have largely focused on the role of microbial mats in providing food resources for the nascent clade. We agree that the early mats would have provided resources and that this would provide the basis for diversification at the microbial level (e.g. Stal, 2012). However, we believe that although the very early stages of animal evolution can be placed within this context, the later stages as multicellularity developed were more heavily dependent on environmental heterogeneity rather than merely on resource availability. Our analysis presents an ecology-based view of the Cambrian explosion that sketches out one view of early animal evolution (for a broader view of such ‘ecosystem engineering’, see Pearce, 2011; Erwin & Valentine, 2013). The earliest stem-group animals were colonial and benthic osmotrophs and filter feeders, competitors for space within a diverse benthic mat ecology. Tiering within their nascent communities led to diversification on an organism scale within the Ediacaran biotas, and this led to an increase in environmental complexity. The resulting heterogeneity of resource distribution, highlighted by a general lack of bioturbation, led to a habitat that would both have facilitated speciation and also led to pressure that favoured

motility (itself a feature inherited from the base of the clade). Widespread mobility and burrowing would itself have greatly added to environmental diversity, in turn leading to the ecological cascade we know as the Cambrian explosion. This analysis largely ignores environmental effects such as changes in sea water composition (Riding, 2011), increased nutrient supply (Derry *et al.*, 1994) and changing oxygen levels (Mills & Canfield, 2014), each possibly associated with tectonic events (e.g. Dalziel, 2014) not because these are unimportant, but their effects must have been filtered through the evolutionary ecological changes we outline above.

V. CONCLUSIONS

(1) Basal animal phylogeny remains unclear, but it is reasonable to regard a monophyletic Porifera as being the sister group to all other metazoans; the old ‘Coelenterata’ are likely to be paraphyletic.

(2) Comparison of Metazoa with their sister group the Choanoflagellata (together forming the Apoikozoa) suggests a pattern of early evolution in animals where the extracellular matrix (ECM) played an important role. This suggests possible body types for the earliest animals in the fossil record.

(3) Although the well-known Ediacaran fossils are problematic, a strong case can be made for regarding early examples as stem-group or early crown-group animals, and younger ones as forming a series of plesions within the Epitheliozoa (i.e. cnidarians, ctenophores, placozoans and bilaterians). The full version of the Vendobionta theory does not seem to be tenable. A comparative approach to the Ediacarans seems likely to be productive in understanding their mutual affinities and broader relationships.

(4) The affinities of *Kimberella* remain highly uncertain, but there seems to be no good reason to regard it as a mollusc; its most likely placement is in the stem-group of the Bilateria.

(5) Ediacarans and bilaterians co-existed for many tens of millions of years, and it is possible that this continued well into the Cambrian. This suggests a much more positive relationship between their respective evolutionary ecologies than traditionally suggested.

(6) The small-scale highly heterogeneous environment generated by Ediacaran ecology would have generated substantial organic carbon resource heterogeneity, and this may have been a proximal cause for the adaptive radiation of the mobile bilaterians and their (otherwise) puzzling burrowing habit. An analogy is drawn with the potential role of resource heterogeneity in the savannah for early hominid evolution.

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