

On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota

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Ediacara fossils document an important evolutionary episode just before the Cambrian explosion and hold critical information about the early evolution of macroscopic and complex multicellular life. They also represent an enduring controversy in paleontology. How are the Ediacara fossils related to living animals? How did they live? Do they share any evolutionary patterns with other life forms? Recent developments indicate that Ediacara fossils epitomize a phylogenetically diverse biosphere, probably including animals, protists, algae, fungi and others. Their simple ecology is dominated by epibenthic osmotrophs, deposit feeders and grazers, but few if any predators. Their evolution started with an early morphospace expansion followed by taxonomic diversification within confined morphospace, and concluded by extinction of many taxa at the Ediacaran–Cambrian boundary.

The Ediacara biota: a retrospect

The newly named Ediacaran Period (635–541 million years ago; Ma) [1] is the youngest geological time interval in the Precambrian. It follows the 635 Ma Marinoan snowball Earth event and precedes the Cambrian Period that is marked by the radiation of bilaterian animals, appearance of complex animal traces and dominance of biomineralizing animals. Within the Ediacaran Period, we see the appearance and global dominance of the Ediacara biota, a distinct group of complex macroscopic organisms that flourished on the eve of the Cambrian radiation of animals [2].

Members of the Ediacara biota were traditionally interpreted as evolutionary precursors to Cambrian animals, including cnidarians, annelids, arthropods and echinoderms [3,4]. A more radical alternative to the traditional interpretation was proposed in the late 20th century. This hypothesis argues, on the basis of their peculiar preservation and inferred functional morphology, that most Ediacara fossils belong to the extinct kingdom Vendobionta, which is characterized by serially or fractally arranged tubular elements and is phylogenetically distant from the Metazoa [5]. The debate continues, and recently both sides have come up with new observations and have conceded that at least some Ediacara fossils represent animals, including bilaterian animals [6–8]. However,

many Ediacara fossils remain phylogenetically unresolved even at the kingdom level.

Glossary

Alternate symmetry: alternate arrangement of segments or tubes or frondlets in the two halves of an Ediacara fossil along a midline. Also known as “symmetry of glide reflection.” Examples include rangeomorphs, erniettomorphs and vendomorphs.

Auteology: branch of ecology that specializes in the study of individual organisms or populations and how they interact with the environment in which they live.

Bilaterian animals: bilaterally symmetric metazoans, including most familiar animals except sponges, cnidarians and ctenophores.

Bodyplan: the blueprint for which important structures of an organism are laid out. Symmetry is an important aspect of bodyplan. Members of a clade at high taxonomic levels typically share a bodyplan, but some bodyplans (e.g. Ediacara fronds) might have evolved convergently.

Crown group: monophyletic group that includes all living members of a clade and their last common ancestor.

Diploblastic animals: animals (e.g. jellyfishes and corals) with only two primary germ layers, the endoderm and the ectoderm, during embryogenesis.

Ediacara fossils: macroscopic and morphologically complex fossils similar to those found in the Ediacara Member of the Flinders Ranges in South Australia. They are geographically worldwide and phylogenetically diverse. Most are found in 575–541 Ma rocks of the late Ediacaran Period.

Ediacaran Period (635–541 Ma): the youngest geological period of the Neoproterozoic Era. It follows the Cryogenian Period of the Neoproterozoic Era and precedes the Cambrian Period of the Paleozoic Era.

Endobenthic: living within sediments.

Epibenthic: living at or just above the water–sediment interface.

Frondose Ediacara fossils: Ediacara fronds consist of two or more leaf-like petalodia typically attached to a stem which is often anchored to the substrate by a holdfast. Previous classification placed all Ediacara fronds in the Phylum Petalonamae [57], but recent analysis suggests that the frond bodyplan represents a convergent response among unrelated benthic taxa to gather nutrients from the water column [25,41,42]. Ediacara fronds are common in Newfoundland, England, Russia, Ukraine, Australia and Namibia.

Morphospace: a representation of form, shape and structure of a group of taxa. Typically, morphological characters are coded for each taxon and multivariate statistical methods are used to represent the data in a two- or three-dimensional space.

Osmotrophic: acquiring nutrients through absorption or osmotic uptake of dissolved organic carbon across membranes.

Stem group: paraphyletic group of extinct lineages that lie outside a crown group but are more closely related to the crown group than to the crown's living sister group.

Synecology: branch of ecology that focuses on the interactions (e.g. predation) between coexisting populations or species.

Taphonomy: the study of the degradation, burial, diagenesis and fossilization of organisms.

Tiering: ecological division of ecospace by benthic organisms of different heights or burrowing depths.

Triploblastic: animals with three primary germ layers (endoderm, mesoderm and ectoderm) during embryogenesis. Examples include all bilaterian animals.

Vendobionta: the kingdom Vendobionta was established by Seilacher [5]. Vendobionts are characterized by tubular structures (“pneus”) that are stitched together like an air mattress. The pneus can be organized serially or fractally. Recently vendobionts have been interpreted as syncytial xenophyphore-like foraminifers [7].

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The phylogenetic uncertainty of Ediacara organisms not only limits their role in testing hypotheses about the tempo of early animal evolution but also compromises our ability to interpret their ecology using modern analogs. Fortunately, ecological inferences can be independently made on the basis of trace fossils, functional morphology and taphonomy. In the past decade, investigation of trace fossils associated with Ediacara body fossils has shed important light on the autecology of several Ediacara taxa, whereas recent advances in the paleoecology of Ediacara organisms [9] are of close relevance to the evolutionary radiation in the Ediacaran–Cambrian transition.

The Ediacaran–Cambrian transition marks a rapid change in taxonomic diversity, morphological disparity and ecosystem complexity of early animals. Does the early evolution of the Ediacara biota share similar patterns with the Cambrian radiation of animals? Only recently have paleontologists begun to approach this question using quantitative methods and a growing database of Ediacara fossils [10,11].

Promising results from emerging research of the phylogenetic affinities, ecological diversity and evolutionary patterns of the Ediacara biota prompt this review. Thus, we will begin with a brief description of the spatial–temporal distribution and bodyplan diversity of the Ediacara biota, followed by a review of recent advances in the phylogenetic, paleoecological and evolutionary analyses of this biota.

Emphasis is restricted to classical Ediacara fossils that are soft bodied, macroscopic and morphologically diverse.

The Ediacara biota in space and time

Ediacara fossils are mostly restricted between 575 and 541 Ma (Figure 1; Box 1). Discoid fossils from the >635 Ma Twitya Formation in northwestern Canada [12] are similar to some simple forms in the Ediacara biota, but the absence of co-occurring complex forms and their significantly older age suggest that the Twitya discs are possibly simple forerunners rather than parts (e.g. hold-fasts) of complex Ediacara fossils. A few Cambrian fossils are interpreted as Ediacara survivors or as phyletic descendants [13,14], but with rare exceptions [14] the most iconic members of the Ediacara biota – the rangeomorphs and erniettaforms (Box 2), for example – are unknown in the Cambrian. It has been proposed that the demise of the Ediacara biota might be due to the closure of a unique taphonomic window mediated by microbial activities [4,15], and that the Ediacara biota continued to thrive after the Cambrian radiation but were simply not preserved. However, the scarcity of Ediacara fossils in exceptionally preserved Cambrian biota such as the Burgess Shale [16] points to a more likely scenario of extinction or at least ecological restriction [2].

The restricted temporal distribution is in contrast with a wide spatial distribution of the Ediacara biota. Ediacara

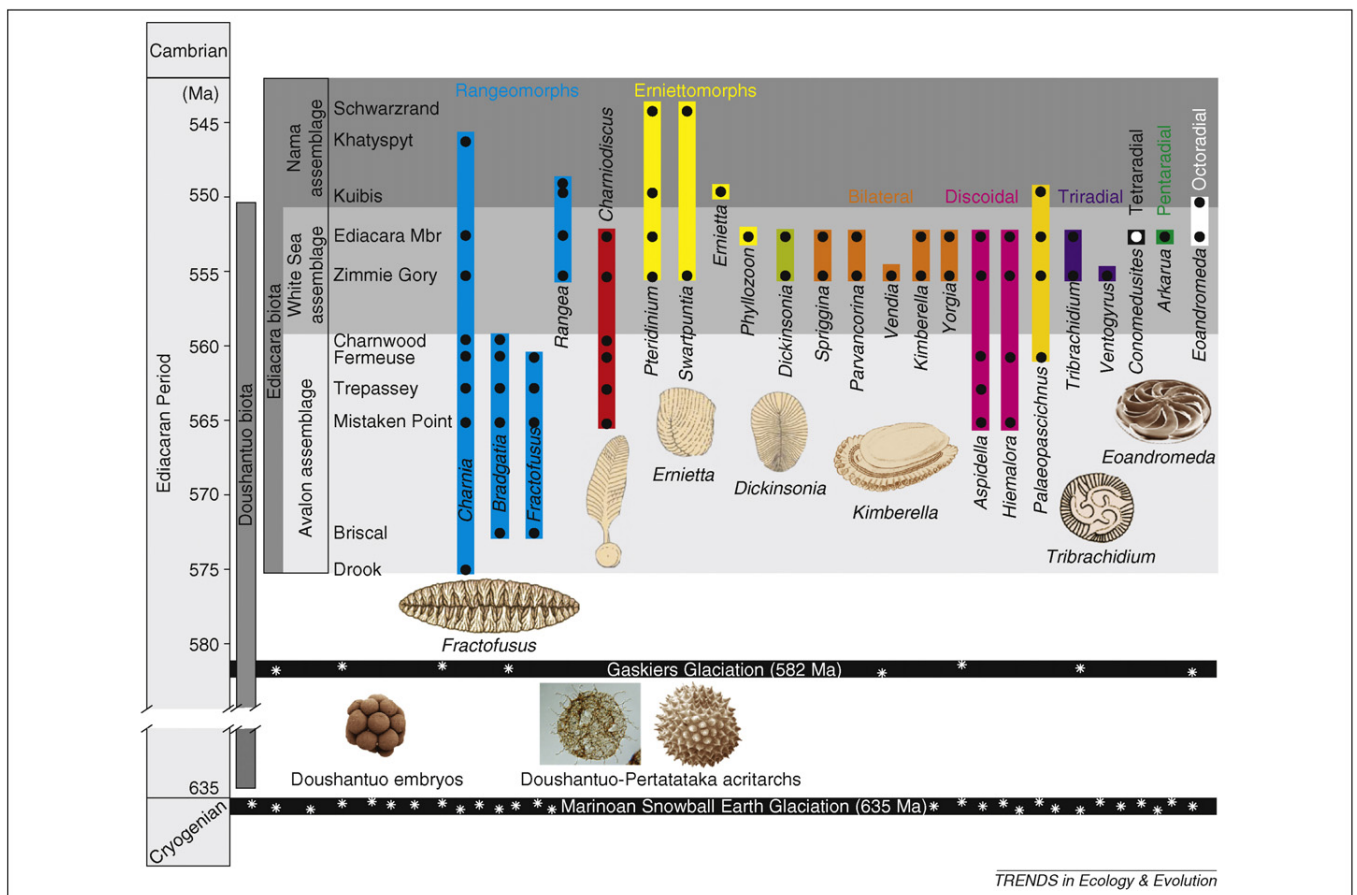


Figure 1. Temporal distribution (bars) and stratigraphic occurrences (black dots) of representative Ediacara genera, plotted against timescale of Ediacaran Period and fossil localities or stratigraphic units. The three Ediacara assemblages (Box 1) are indicated by different shades of gray. The Marinoan and Gaskiers glaciations, as well as the age range of the Doushantuo biota, are also marked. Modified from Ref. [58] with permission from the AAAS.

Box 1. The three Ediacara assemblages

Once believed to be rare, Ediacara fossils are now known from over 40 localities worldwide, and are temporally and ecologically grouped into three well-defined assemblages based on cluster analysis: the Avalon, White Sea and Nama assemblages [10].

The Avalon assemblage (575–560 Ma) is represented by fossils from the Conception Group in Newfoundland and equivalent rocks in England [59,60] and dominated by rangeomorphs and cosmopolitan forms such as *Charniodiscus* [41,42]. The Avalon organisms lived in a deep-water environment following the 580 Ma Gaskiers glaciation [59] at a time when the deep ocean began to be ventilated [61]. The Avalon fossils are preserved as *in situ* communities that were buried underneath episodic ash falls [2]. No trace fossils are known from the Avalon assemblage.

The White Sea assemblage (560–550 Ma) is exemplified by Ediacara fossils from the Flinders Ranges of South Australia and the White Sea coast of Russia. It contains the highest taxonomic diversity, the first probable examples of stem-group bilaterian animals [8] and the first unambiguous traces made by motile animals [34]. Ediacara fossils in the Flinders Ranges area are mostly restricted to a single stratigraphic unit (the Ediacara Member of the Rawnsley Quartzite) deposited in a shallow-water, offshore ramp setting [62]. The best-preserved and most-diverse Ediacara fossils in the White Sea area occur in 558–555 Ma rocks that were deposited in a shallow-water, marine-dominated environment above storm wave base [63]. Preservation of Ediacara fossils in both the Flinders Ranges and White Sea areas was aided by vast expanses of microbial mats that covered Ediacaran seafloors, accelerated fossilization and resulted in the casting and molding of Ediacara organisms [15].

The Nama assemblage (550–541 Ma), best known in the Kuibis and Schwarzrand subgroups of Namibia, includes several rangeomorphs and erniettomorphs (Figure 1) [44,64,65]. The Nama assemblage also includes the oldest representatives of biomineralizing animals such as *Cloudina* and *Namacalathus* [17]. Nama fossils are preserved by three-dimensional casting within fine-grained storm or mass-flow event-beds that were deposited in shallow wave- or storm-dominated environments [64].

These assemblages are interpreted as representing three different evolutionary stages of the Ediacara biota [10]. Although these assemblages might in part represent different ecological associations controlled by environmental factors [63], taxonomic turnover among these assemblages (Figure 1) and geochronological data indeed support the idea that they represent three stages of Ediacara evolution.

fossils have been recovered from nearly 40 localities in several sedimentary basins around the world [17]. Among these, four main localities representing three main assemblages (the Avalon, White Sea and Nama assemblages; see Figure 1 and Box 1) account for much of the known Ediacara taxonomic and morphological diversity.

Bodyplans in the Ediacara biota

Despite a global distribution and over 35 million years of evolutionary history, the overall taxonomic diversity of the Ediacara biota is surprisingly low, estimated to be a little over 100 species worldwide [10]. In stark contrast, morphological disparity is surprisingly high [11], with unique morphologies never to be repeated in the Phanerozoic [18]. This has resulted in a 'bottom-up' classification scheme, in which the overwhelming majority of Ediacara genera are monospecific, and no general consensus about high-level classification is available. Recent attempts at classifying the Ediacara biota in high-level taxonomic groups have avoided shoehorning these peculiar fossils into Phanerozoic phyla [3]. Instead, emphasis has been

placed on the unique bodyplans (symmetry and constructional architecture; Box 2) shared by Ediacara fossils [19]. The combination of low species diversity, high bodyplan diversity and lack of modern analogs poses a significant challenge to the phylogenetic placement of Ediacara fossils.

Phylogenetic diversity

Ediacara fossils have traditionally been compared with extant animals and interpreted as stem-group, crown-group and sometimes highly derived members of animal phyla [3]. For example, *Palaeophragmodictya* has been interpreted as a hexactinellid sponge [20], whereas several discoidal forms have been interpreted as hydrozoans, jellyfishes or other diploblastic animals. The famous frondose fossils *Charniodiscus* (Box 2, Figure 1a) and *Charnia* (Box 2, Figure 1c) were regarded as colonial octocorals [21], *Rangea* (Box 2, Figure 1b) as an octocoral [21] or a stem-group ctenophore [22], *Dickinsonia* (Box 2, Figure 1g) and *Spriggina* (Box 2, Figure 1i) as polychaetes, *Parvancorina* (Box 2, Figure 1f) and *Praecambridium* as arthropods, the pentaradial *Arkarua* (Box 2, Figure 1k) as an echinoderm [23] and the fenestrate *Ausia* as a tunicate chordate [17].

Taken at face value, the traditional interpretations would imply that the Ediacara biota was dominated by cnidarians. However, many discoidal Ediacara organisms could not have functioned as jellyfishes [5]. Instead, some might represent anchoring structures of erect epibenthic organisms such as *Charniodiscus* and *Charnia* [24,25], whereas others might be microbial colonies [26]. Closer examination of *Charnia*, *Rangea* and *Charniodiscus* also shows that their lateral branches are not morphologically homologous with polyp leaves of modern colonial octocorals (e.g. pennatulaceans). Their branches were either stitched together or attached to a membranous sheet. Thus, water flow between branches was restricted and the branches cannot be functionally analogous to polyp leaves of the filter-feeding pennatulaceans either. Additionally, their growth dynamics is distinct from that of pennatulaceans, and the fractal frondlets of Ediacara rangeomorphs are unlike polyp leaves of extant pennatulaceans [5,18,27]. However, such differences from modern pennatulaceans do not by themselves preclude the possibility for these frondose Ediacara organisms to be stem-group cnidarians or stem-group eumetazoans [28].

By contrast, the case of bilaterian animals in the Ediacara biota has been strengthened by recent discoveries. The bilaterally symmetric fossil *Kimberella* shows evidence for anterior–posterior and dorsal–ventral differentiation, satisfying some basic criteria of bilaterian animals. In addition, *Kimberella* fossils are associated with radular marks (Box 2, Figure 1e), suggesting that it might have grazed upon microbial mats [8]. Body fossils of another Ediacara form, *Yorgia*, have been found together with a series of resting traces made by the same individual, suggesting intermittent relocation [29]. *Dickinsonia*, which has variously been interpreted as a cnidarian [30], a polychaete [3], a vendobiont [5–7] or a lichen [31], is also associated with intermittent resting traces (Box 2, Figure 1h) and shows evidence for muscular contraction (Box 2, Figure 1g) [4,32].

Despite growing evidence for the presence of bilaterian animals in the Ediacara biota, their phylogenetic placement within the bilaterian tree is uncertain. *Kimberella* has the best phylogenetic resolution so far and is interpreted as a possible mollusc [8]. Another Ediacara fossil, *Ausia*, is placed in the urochordates [17], although detailed analysis has not been published. Other purported bilaterians, including *Yorgia*, *Dickinsonia*, *Parvancorina* and *Vendia*, lack diagnostic features such as a mouth or digestive tract [32], despite earlier claims of their presence [4,21,29]. Evidence for molting has not been reported for the presumed arthropods *Parvancorina* and *Praecambridium*. In other cases, the inferred diagnostic features (e.g. segmentation and parapodia in the purported annelids *Dickinsonia* and *Spriggina*) are subject to interpretation. Because of such ambiguities, cladistic verification of the phylogenetic affinities [33] remains on a weak footing. Burrowing traces in late Ediacaran (560–541 Ma) rocks [34] do imply the presence of coelomate bilaterians, but do not add to phylogenetic resolution given that coeloms might have evolved independently in protostomes and deuterostomes [35]. Thus, many bilateral forms in the Ediacara biota might represent stem-group bilaterians that are scattered between the cnidarian–bilaterian divergence and the base of crown-group bilaterians (Figure 2).

The rangeomorphs and erniettomorphs continue to defy phylogenetic interpretation. They share the vendobiont bodyplan [5–7] that is characterized by alternately arranged tubular or frondlet modules on two or more vanes. Rangeomorphs are further characterized by their fractal body architecture [18]. Although rangeomorphs and erniettomorphs might be natural groups and the best candidates for a vendobiont construction [4,32], their phy-

logenetic placement is uncertain. Alternate symmetry and fractal architecture depart from extant bilaterian bodyplans. The interpretation of some rangeomorphs and erniettomorphs as pennatulacean-like octocorals [21], ctenophores [22] or giant deep-sea xenophyophore foraminifers [6,7] has met with criticism on the grounds of ontogeny and functional morphology [5,18,27]. Thus, it seems that rangeomorphs and erniettomorphs lie outside the crown-group bilaterian clade; they could be stem-group metazoans (Figure 3) or eumetazoans [28].

Many other Ediacara fossils remain in phylogenetic limbo. Tri-, tetra-, penta- and octoradial forms are little constrained phylogenetically because of the lack of close modern analogs. Possibly these forms represent a variety of body symmetries that arose during the evolutionary course from radially symmetric sponges to bilaterally symmetric triploblastic animals, and only bi-, tetra- and octoradial symmetries survive in modern diploblastic animals. If true, these Ediacara forms are mostly extinct, diploblastic-grade branches between sponges and crown-group bilaterians (Figure 2). The diversity of body symmetry implies greater developmental versatility among early diploblastic-grade animals than cnidarians that have survived to the present day [28]. This scenario is intriguing given the complex genomes that are still present in some modern diploblastic animals such as sea anemones [36].

There are also several tubular or ribbon-shaped fossils that were traditionally interpreted as trace fossils but are more likely body fossils [37]. Some could be algae [32], but their morphological simplicity does not allow conclusive phylogenetic inferences. Still other Ediacara fossils, including some discoidal forms, have been cautiously interpreted as marine fungi [38], but definitive evidence is lacking.

Box 2. Bodyplans in the Ediacara biota

Morphological construction of the Ediacara biota consists of a vast range of bodyplans, including an array of peculiar constructions never repeated after the Cambrian explosion. These bodyplans are described below and some examples are illustrated in Figure 1.

Rangeomorphs (Figure 1b,c) consist of fractally quilted Ediacara organisms [7] with frondlets arranged to form a repetitive, self-similar pattern [18]. Frondlets are organized to build a diverse array of higher-order morphologies, including the spindle-shaped *Fractofusus*, cabbage-shaped *Bradgatia*, comb-shaped *Pectinifrons* and leaf-shaped *Rangea* (Figure 1b) and *Charnia* (Figure 1c). Rangeomorphs are likely monophyletic and unique to the Ediacara biota. They were probably epibenthic osmotrophs.

Erniettomorphs (Figure 1d) have biserially quilted tubes that are alternately arranged along a midline [7]. They are not bilaterally symmetric. Examples include the bag-shaped *Ernietta*, ribbon-shaped *Phyllozoon*, boat-shaped *Pteridinium* and multifoliate frond *Swartpuntia* (Figure 1d). *Dickinsonia* (Figure 1g,h) might belong to this group [58], but its truly bilaterally symmetry, capability of intermittent locomotion [32] and subtle anterior–posterior differentiation suggest that it might be closer to bilateral forms described below.

Bilateral forms (Figure 1e,f,i) are characterized by anterior–posterior differentiation with a differentiated ‘head’ region. Examples include segmented forms such as *Spriggina* (Figure 1i) and *Yorgia*, shield-shaped *Parvancorina* (Figure 1f) and mollusc-like *Kimberella* (Figure 1e). Most are bilaterally symmetric, but some (e.g. *Vendia*) seem to have alternate symmetry. *Kimberella* was dorsal–ventrally differentiated [8]. *Kimberella* and *Yorgia* were probably motile [8,29]. Bilateral

forms probably belong to a paraphyletic group from which crown-group bilaterian animals arose.

Discoidal forms are characterized by concentric and sometimes radial features. They are polyphyletic and widely distributed. Some are holdfast structures associated with erect frondose forms [24,25,46,60,66,67], but others might represent microbial colonies [26].

Palaeopascichnids consist of straight, sinuous and sometimes branching series of crescent, spherical, ellipsoidal or discoidal elements. Examples include *Palaeopascichnus*, *Yelovichnus* and possibly *Funisia* [68]. Traditionally interpreted as trace fossils [19], they are more likely body fossils [6,34,56,69].

Triradial forms (Figure 1j) are characterized by triradial symmetry or consist of three spiral arms. Examples include *Albumares*, *Anfesta*, *Tribrachidium* (Figure 1j), *Triforillonia* and possibly *Rugoconites*.

Tetradial forms are rare and include *Conomedusites* from South Australia, which is characterized by its four radiating grooves dividing its discoidal body into four lobes. It might be related to Cambrian conulariid cnidarians [3].

Pentradial (Figure 1k) forms are represented by *Arkarua* (Figure 1k) from South Australia, which is characterized by a five-fold symmetry and interpreted as a stem-group echinoderm [23].

Octoradial forms include *Eoandromeda*, which consists of eight spiral arms tightly wrapped into a disc [70].

Differentiating convergence from homology in forms that have no modern counterparts has resulted in many controversies in the classification and phylogenetic placement of Ediacara fossils. This task remains the single most important goal of Ediacaran paleontology.



TRENDS in Ecology & Evolution

Figure 1. Disparate bodyplans and unique morphologies of the Ediacara biota. **(a)** *Charniodiscus* frond with a circular holdfast and a large petalodium leaf. **(b)** *Rangea* displaying fractal, repetitive primary branches and rangeomorph frondlets. **(c)** Incompletely preserved *Charnia* frond with rectangular modular units within which rangeomorph frondlets reside. **(d)** *Swartpuntia* frond. **(e)** *Kimberella* (white arrow) with *Radulichnus* grazing traces (black arrow). **(f)** *Parvancorina* with bilateral symmetry and anterior–posterior differentiation. **(g)** *Dickinsonia* displaying shrinkage marks possibly due to muscle contractions. **(h)** A series of three *Dickinsonia* resting traces (1 = oldest; 3 = youngest) presumed to have been made by one individual. **(i)** *Spriggina* with bilateral symmetry, anterior–posterior differentiation and possible segmentation. **(j)** *Tribrachidium* with triradial symmetry. **(k)** *Arkarua* with pentaradial symmetry. Scale bars represent 1 cm. Photos (a,e,f,g,h) are provided by J. Gehling, and (b,d) by G. Narbonne.

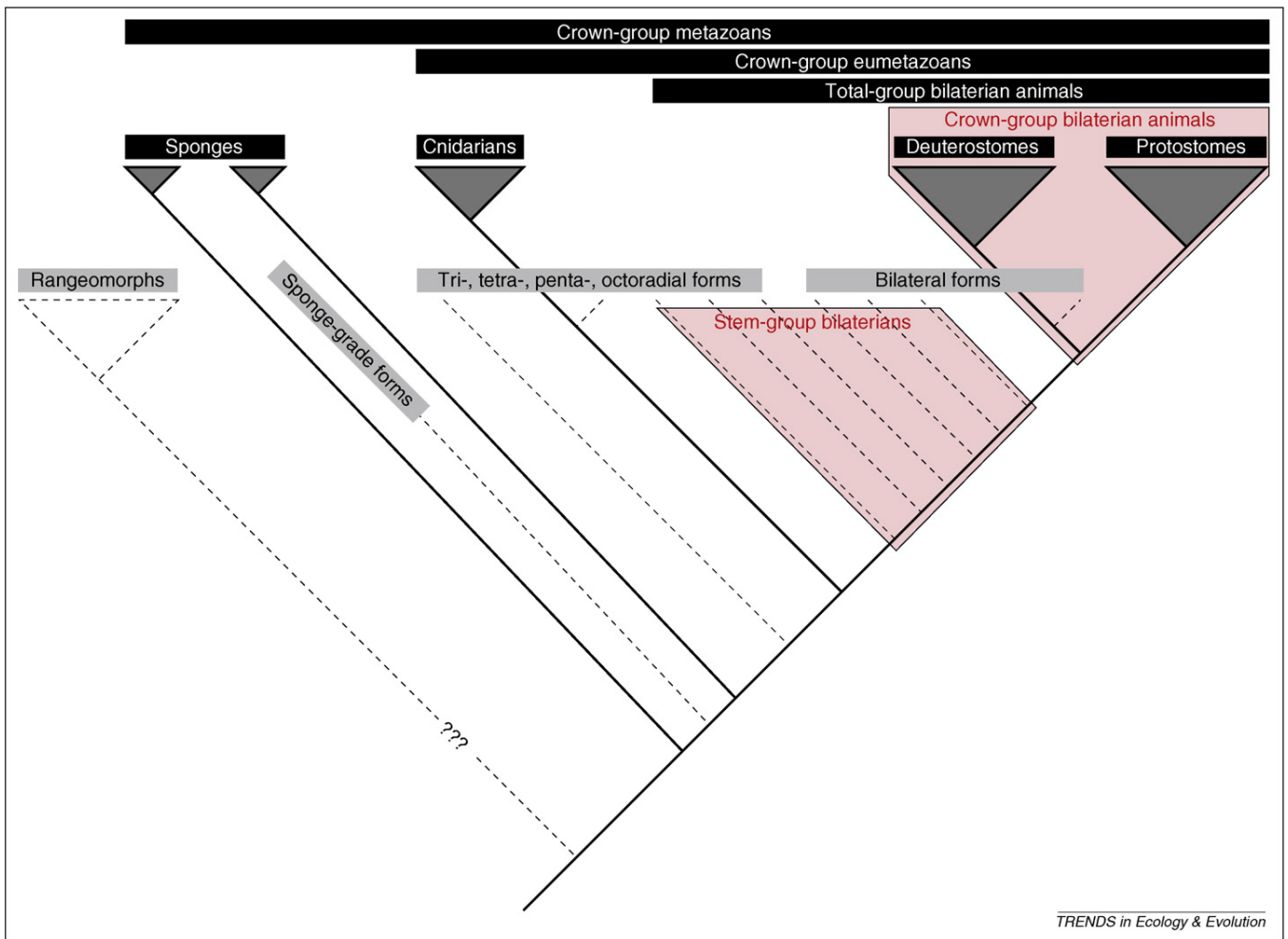


Figure 2. Possible phylogenetic placement of bilateral Ediacara fossils (vendomorphs, parvancorinomorphs, *Yorgia*, *Kimberella* and *Dickinsonia*), tri-, tetra-, penta- and octoradial forms, and rangeomorphs in the metazoan tree. The diverse array of morphological constructions exemplified by the Ediacara biota suggests a greater phylogenetic diversity than typically assumed. Ediacara fossils are represented by dotted lines or triangles, extant animals by gray triangles.

To summarize, it is important to realize that the Ediacara biota consists of an assortment of phylogenetically diverse taxa, possibly ranging from microbial colonies, algae, fungi and protists to animals, including bilaterian animals [2,39,40]. Just as important, the Ediacara biota likely comprises stem-group members of various extant clades. These stem groups might have some, but not all features that collectively define extant crown clades. Therefore, extreme approaches to push Ediacara fossils into the crown-group Metazoa on the basis of plesiomorphies, or to relegate them into the phylogenetically distant Vendobionta because of the lack of crown-group synapomorphies, are equally undesirable. Given the phylogenetic uncertainties of many Ediacara fossils, paleoecologists are facing a daunting task to understand the ecological make-up of Ediacara communities using modern analogs.

Ecological diversity

Some Ediacara fossils appear to be preserved where they lived, which offers exceptional opportunities for analysis of community ecology. Such analyses [41–43] show that most members of the Ediacara biota were epibenthic organisms, with a few possible examples of shallow endobenthic (entirely buried; *Pteridinium*) and semi-endobenthic

(half-exposed and half-buried; *Ernietta*) organisms [44,45]. Additional evidence for epibenthic and endobenthic activities comes from shallow burrows and sediment surface traces [34], but there is no convincing evidence for pelagic or deep endobenthic animals.

Perhaps the most noticeable ecological difference from Phanerozoic epibenthic communities is the dominance of sessile organisms in the Ediacara biota. All rangeomorphs appear to have been nonmotile, typically attached to a holdfast (e.g. *Charnia*) [46] or lying freely on the seafloor (e.g. *Fractofusus*) [47]. Many other Ediacara fossils, including *Palaeophragmodictya*, tri-, tetra-, penta- and octoradial forms, are also likely to have been attached or freely lying on the seafloor. Although vendomorphs and parvancorinomorphs were interpreted as relatives of arthropods, there is no convincing evidence for motility. *Yorgia* and *Dickinsonia* moved intermittently, facultatively and perhaps passively. Only *Kimberella* seems to have actively pushed sediments during self-powered movement [8,32]. The subordinate role of motile animals is also supported by the lower abundance and diversity of trace fossils in Ediacaran rocks than in Phanerozoic rocks [34].

Although Ediacara communities were likely supported by cyanobacterial and algal primary producers [48], the

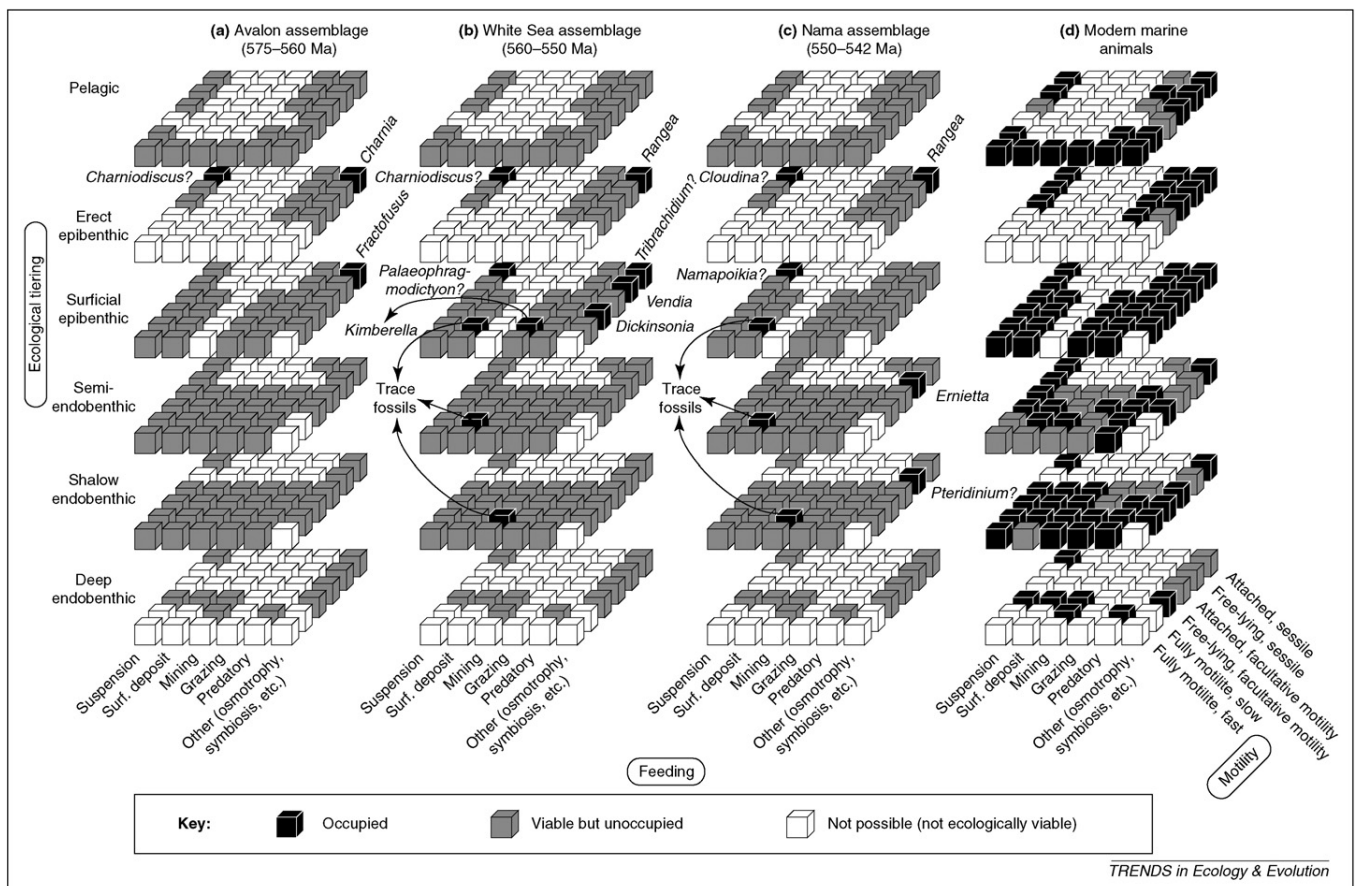


Figure 3. Ecospace occupancy in the three Ediacara assemblages, as compared with modern animals. Theoretical ecospace is represented in $6 \times 6 \times 6$ cubes along three axes (tiering height, feeding and motility). Of the 216 theoretical cubes, 118 are ecologically viable [9]. In modern marine faunas, 92 of the 118 cubes (~78%) are filled. In comparison, ecospace occupancy in Ediacara assemblages is only ~10%, suggesting that the ecological structure of the Ediacara biota is much simpler. Modified from Ref. [9] with permission from the Palaeontological Association.

scarcity of predation and parasitism suggests that food chains were much shorter and ecological interactions much simpler, when compared to modern epibenthic communities. Vendobiont proponents have proposed that Ediacara organisms housed photosynthetic or chemosynthetic endosymbionts in their syncytial cytoplasm [49], although photosynthetic endosymbionts can be ruled out for Ediacara organisms from deep-water (below the photic zone) communities in Newfoundland and northwestern Canada. Many Phanerozoic heterotrophic feeding styles, including predation, filtering and deep burrowing, are either absent or poorly represented in the Ediacara biota. One possible filter feeder is the putative sponge *Palaeophragmodictya* [20], but functional morphology evidence in support of its active filtering is unknown. *Kimberella* that grazed upon microbial mats was probably one of the most active feeders. Given their intermittent motility, it is unlikely that *Dickinsonia* and *Yorgia* were grazers or deposit feeders. Instead, they were probably osmotrophic organisms that absorbed nutrients through their sole surface [32], which was in close contact with microbial substrates. The absence of a mouth and digestive tract in vendobionts, parvancoriniforms, erniettomorphs and rangeomorphs suggests that they might also have been osmotrophs. Indeed, the fractal architecture of rangeomorphs might be an adaptation to increase surface area for osmotrophy [50].

In light of their possible osmotrophic feeding strategy, it is not surprising that most Ediacara organisms lived near the water–sediment interface and were closely associated with microbial mats [15], where dissolved nutrients were abundant. Most epibenthic organisms in Ediacara communities from Newfoundland [41,42] were <20 cm above the sediment surface and very tall epibenthos were extremely rare, possibly owing to decreasing concentration of dissolved nutrients away from the water–sediment interface. Furthermore, taller epibenthos only occurred in later stages of ecological succession, possibly owing to increasing competition in more mature communities that drove some osmotrophs away from the water–sediment interface and resulted in resource partitioning.

To summarize, Ediacara communities were dominated by sessile epibenthos and their ecological structures were relatively simple. This simplicity is visualized in a creative analysis [9] which shows that, in comparison with modern ecosystems, ecological diversity was an order of magnitude lower in Ediacara assemblages (Figure 3), even in Newfoundland and South Australia where near-census populations were preserved *in situ* [41–43].

Macroevolutionary patterns

Although the Ediacara biota does not represent a monophyletic clade, it is still possible to document its macro-

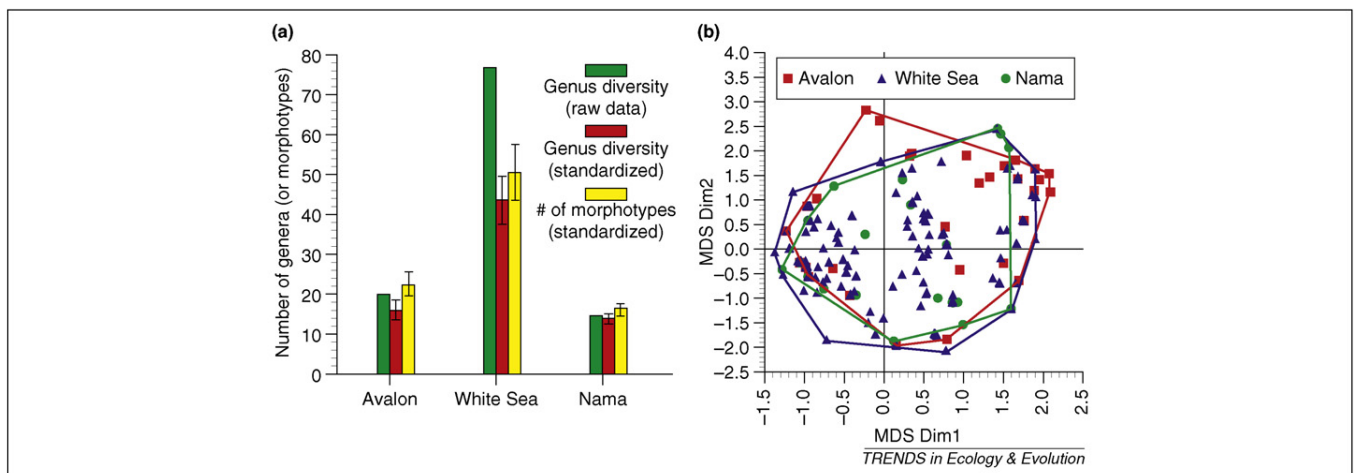


Figure 4. Taxonomic diversity versus morphospace range of the three Ediacara assemblages. Morphospace range was nearly fully established early in the evolution of the Ediacara biota (Avalon assemblage), and remained similar throughout the history of the Ediacara biota. Fluctuation in taxonomic diversity of younger Ediacara assemblages (White Sea and Nama) occurred within the established morphospace. (a) Taxonomic diversity estimated as number of genera (with or without sampling intensity correction) or morphotypes (unique combination of morphological characters). Error bars represent 95% confidence intervals estimated by 1000 independent rarefaction runs. (b) Morphospace ranges depicted by convex polygons. Morphometric analysis was carried out using the multidimensional scaling method. Modified from Ref. [11].

evolutionary patterns. Given that the Ediacara biota marks the early evolution of macroscopic life forms with complex and diverse morphologies, it is crucial to ask whether Ediacara biodiversity emerged and went extinct abruptly. Such patterns give insights into evolutionary processes and mechanisms. Similar questions have been posed to the Cambrian explosion of animals, but the Ediacara biota has a unique advantage in that it encompasses a broader phylogenetic range than Cambrian animals.

The most straightforward way to characterize macroevolutionary patterns is to quantify taxonomic diversity. Quantitative studies [11] demonstrate that taxonomic diversity of the White Sea assemblage is at least twice greater than the other two Ediacara assemblages even after correction for sampling intensities (Figure 4). Analysis of morphospace range, however, paints a different picture [11]. Nonparametric multidimensional scaling analysis showed that the older Avalon assemblage occupied a morphospace range that is similar to those occupied by the younger White Sea and Nama assemblages (Figure 4). This analysis implies that the morphospace range was maximized during the Avalon explosion when taxonomic diversity was low – a pattern that is similar to morphospace evolution during the Cambrian explosion [51]. By contrast, taxonomic diversification in the White Sea assemblage occurred within a defined morphospace range, leading to more crowdedness within previously defined morphological constraints. Furthermore, taxonomic reduction in the Nama assemblage did not cause morphospace contraction. This pattern implies morphological saturation and constraint in Ediacara evolution. That morphospace occupation tends to precede taxonomic diversification appears to be a common macroevolutionary pattern that has been seen in the evolutionary history of animals and other eukaryotes [51,52]. This similarity indicates that the evolutionary mechanisms responsible for the decoupled morphological and taxonomic patterns are unlikely to be intrinsic to a specific clade of eukaryotic life.

The disappearance of the Ediacara biota near the Ediacaran–Cambrian boundary represents a fundamental biotic change; the necessary phylogenetic continuity of animals, fungi and algae across the boundary do not minimize the significance of this extinction. However, the pattern and mechanism of this biotic change are little known. Currently available data do not have the resolution to tell whether the extinction was gradual, stepwise or abrupt. In turn, the poorly documented pattern limits our ability to test whether the extinction was caused by an oceanic anoxia [53] or an increase in macroscopic predation [54] at the Ediacaran–Cambrian boundary.

Summary and prospect

The Ediacara biota bridges the cryptic evolution of multicellular life in the early Ediacaran and the extraordinary radiation of animals in the Cambrian Period. Many phylogenetic, evolutionary and ecological questions related to the rise of animals have their answers embedded in the Ediacara biota. The Ediacara biota is phylogenetically greater than the Metazoa or Vendobionta. A variety of phylogenetically diverse organisms might be represented in the Ediacara biota, including many stem-group members of extant clades. To fully resolve their phylogenetic affinities, future investigations should focus on exploring diverse taphonomic windows, including carbonaceous shales [48], carbonates [55] and cherts [56], which might provide complementary morphological, taphonomic and ecological insights. With better-resolved morphology comes better understood homology. Only then can rigorous cladistic methods be applied to test competing hypotheses about the phylogenetic affinities of the Ediacara biota.

The Ediacara biota appears to be dominated by sessile epibenthic osmotrophs, and many modern feeding modes are absent or poorly represented (Figure 3). However, ecological investigation of the Ediacara biota is still in its infancy, and the autecology and synecology of many Ediacara taxa remain unknown. More complete knowledge about the three-dimensional anatomy, functional

morphology and paleoenvironments might place further constraints on Ediacara ecology, which in turn has important implications for Earth system evolution (e.g. biological cycling of carbon and oxygenation) in the late Ediacaran Period [50].

The evolution of Ediacara morphospace follows patterns similar to the Cambrian explosion, but we still know very little about the macroevolutionary patterns of the Ediacara biota. As the Ediacara database grows, we should attempt a synthetic analysis and ask general questions about macroevolutionary patterns such as paleobiogeographic differentiation, latitudinal diversity gradients and mass extinction. Only when these patterns are fully characterized can we test hypotheses about the processes, causes and consequences of Ediacara evolution.

Disclosure statement

The authors disclose no actual or potential conflict of interest including any financial, personal or other relationships with other people or organizations within three (3) years of beginning this work that could inappropriately influence (bias) their work.

Acknowledgements

We thank M. Brasier, M. Fedonkin, J. Gehling, J. Huntley, M. Kowalewski, G. Narbonne and B. Shen for useful discussions and providing illustrations used in this paper. Two anonymous reviewers greatly enhanced the quality of the manuscript. Research was supported by the NSF Sedimentary Geology and Paleobiology Program, NASA Exobiology and Evolutionary Biology Program, National Natural Science Foundation of China and an NSERC Fellowship.

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