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THE EDIACARA BIOTA: Neoproterozoic Origin of Animals and Their Ecosystems

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■ **Abstract** The Ediacara biota (575–542 Ma) marks the first appearance of large, architecturally complex organisms in Earth history. Present evidence suggests that the Ediacara biota included a mixture of stem- and crown-group radial animals, stem-group bilaterian animals, "failed experiments" in animal evolution, and perhaps representatives of other eukaryotic kingdoms. These soft-bodied organisms were preserved under (or rarely within) event beds of sand or volcanic ash, and four distinct preservational styles (Flinders-, Fermeuse-, Conception-, and Nama-style) profoundly affected the types of organisms and features that could be preserved. Even the earliest Ediacaran communities (575–565 Ma) show vertical and lateral niche subdivision of the sessile, benthic, filter-feeding organisms, which is strikingly like that of Phanerozoic and modern communities. Later biological and ecological innovations include mobility (>555 Ma), calcification (550 Ma), and predation (<549 Ma). The Ediacara biota abruptly disappeared 542 million years ago, probably as a consequence of mass extinction and/or biological interactions with the rapidly evolving animals of the Cambrian explosion.

INTRODUCTION

Life first appeared on Earth at least 3.5 billion years ago, but the first 3 billion years were dominated by microbial, especially prokaryotic, organisms and ecosystems (see review in Knoll 2003). The Ediacara biota (575–542 Ma) marks a pivotal position in the evolution of life, the appearance of the first large and architecturally complex organisms in Earth history. In contrast with the microscopic fossils that dominate most Precambrian fossil assemblages, Ediacara-type fossils are typically in the centimeter to decimeter range, with some giants ranging to more than a meter in length. The diversity of shapes in the Ediacara biota include discs, fronds, and segmented morphologies at least vaguely comparable with modern animals, alongside bizarre fractal constructions unknown in our modern world. Well-preserved Ediacaran assemblages typically occur in abundances that are similar to those of animals in modern marine ecosystems, with some Ediacaran fossil surfaces containing densities of 3000–4000 individuals per square meter, comparable with the most productive modern marine ecosystems.

The first recognition and description of fossils now attributed to the Ediacara biota was by Billings (1872), who named and described *Aspidella terranovica* based on centimeter-scale discoid impressions that occur in unbelievable abundances in Neoproterozoic strata of the Fermeuse Formation in eastern Newfoundland. Billings recognized that *Aspidella* was nonmineralized; that it occurred in undoubted Proterozoic strata, stratigraphically several kilometers below the base of the Cambrian; and that it did not resemble any described Phanerozoic fossils. However, most of Billing's contemporaries and successors were less receptive to the concept of Precambrian megascopic life, and over the subsequent century, *Aspidella* was largely relegated to lists of inorganic sedimentary structures. Only recently has *Aspidella* been accepted as a biological feature that probably represents the base of an Ediacaran frond (Gehling et al. 2000). Similarly, Ediacara-type fossils in Namibia in southern Africa (Gürich 1933), and even the classic discoveries at Ediacara in South Australia (Sprigg 1947, 1949), originally were ascribed to the Early Cambrian on the grounds that this level of organic complexity was unknown from Precambrian fossils. Glaessner (1959) recognized that similar fossils from Australia, Namibia, and England were part of a single, widespread biota that characterizes the terminal Proterozoic, and he coined the term "Ediacara fauna" for this biota.

The Ediacara biota has now been reported from nearly 30 localities on 5 continents (Narbonne 1998, figure 3). A low diversity assemblage of "Twitya discs" occurs immediately below Marinoan glacial deposits in northwestern Canada (Hofmann et al. 1990), and a handful of possible "Ediacaran survivors" have been described from Cambrian strata (e.g., Conway Morris 1993, Jensen et al. 1998, Hagadorn et al. 2000), but all diverse occurrences of the Ediacara biota postdate the highest Neoproterozoic glacial diamictites and predate the base of the Cambrian (Figure 1). This stratigraphic relationship has obvious evolutionary implications, and forms the basis of the newly defined "Ediacaran Period" (Knoll et al. 2004). The unique biology, ecology, and taphonomy of the Ediacara biota effectively marks the end of the Proterozoic Eon and heralds the beginning of the Phanerozoic.

PRECURSERS AND TRIGGERS TO EDIACARAN COMPLEXITY

Biotic Prelude

Evidence from fossils and biomarkers suggests that eukaryotes first appeared 1.8–2.7 billion years ago, but their evolution remained highly conservative throughout much of the Proterozoic (Knoll 2003). Crown-group members of the red algae, yellow-brown algae, green algae, heterokonts, and testate amoebae had appeared by 750 Ma (Butterfield 2004), but animals seem to have evolved relatively late

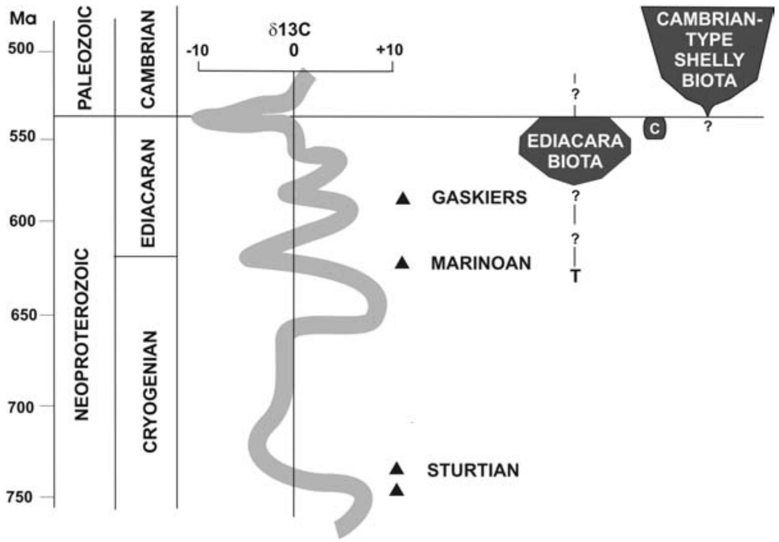

Figure 1 Stratigraphic setting of the Ediacara biota in relation to Neoproterozoic global change [carbon isotopes and global glaciations (▲)] and major evolutionary events. "T" marks the position of the Twitya discs; "C" marks the position of Ediacaran calcified metazoans.

in the Proterozoic. Suggestions that triploblastic animals appeared more than 1600 Ma based on putative worm burrows (Seilacher et al. 1998, Rasmussen et al. 2002) are not substantiated by the illustrated structures or by the apparent billion-year gap between these structures and the oldest undoubted animal fossils (Conway Morris 2002, Jensen 2003). The best molecular clock estimates for the last common ancestor of the bilaterians vary by a factor of two, from ca. 1200 Ma to ca. 600 Ma, with most recent estimates focusing on the younger end of this spectrum (Peterson et al. 2004, Douzery et al. 2004). The radial phyla (sponges and cnidarians) are morphologically, developmentally, and genetically simpler than the Bilateria, and their origin must predate these molecular estimates (Valentine 2002).

The discovery of fossilized cnidarian and possibly bilaterian eggs and embryos (Xiao et al. 1998, Xiao & Knoll 2000) in phosphorites of the Doushantuo Formation of China represents a significant development in Ediacaran paleobiology. Datable volcanic ash beds have not yet been reported from the Doushantuo Formation, but less-reliable Pb-Pb and Lu-Hf dates on phosphates (599–584 Ma; Barfod et al. 2002) suggest that the Doushantuo eggs and embryos may be slightly older than the oldest known Ediacara-type fossils.

From the above, it is obvious that the Ediacara biota does not reflect the first appearance of either modern-style, crown-group eukaryotes (which had occurred among the algae 300–600 million years earlier) or the oldest animals (which probably appeared in microscopic form at least several tens of millions of years earlier). Instead, the Ediacara biota reflects the achievement of large size and architectural complexity in animals, indeed in life, for the first time in Earth history. Present evidence suggests that this profound evolutionary event was precipitated by the equally profound physical and chemical global changes that wracked the Neoproterozoic Earth.

Neoproterozoic Global Change

Available paleontological evidence and the most recent molecular dates imply that animals arose at a critical time in Earth evolution, during the breakup and dispersal of the supercontinent Rodinia. Views of the configuration of Rodinia vary considerably, but most workers agree that it formed approximately 1000–1200 Ma and broke up at approximately 750 Ma (see papers in Kah & Bartley 2001). This tectonic engine drove major changes in the hydrosphere, atmosphere, and cryosphere that led to equally profound changes in the biosphere.

The most significant impact of the breakup of Rodinia was the appearance, for the first time in more than a billion years, of widespread glaciation (Hoffman & Schrag 2002). Modern thinking is converging around the idea that at least three major Neoproterozoic glaciations (Figure 1) can be distinguished on the basis of C- and Sr-isotope profiles in underlying and overlying strata, distinctive cap carbonates, and available U-Pb dates: the Sturtian (ca. 710–725 Ma), the Marinoan (ca. 635–600 Ma), and the Gaskiers (580 Ma). The Sturtian and the Marinoan were perhaps the greatest glaciations Earth ever experienced, with reliable paleomagnetic evidence of glaciers at sea level within 10° of the equator (Evans 2000). The extent of ice cover during these glaciations is controversial. Some models have proposed a "hard snowball," with ice up to 1 km thick covering the entire surface of the world's oceans (e.g., Hoffman & Schrag 2000), but others favor a "soft snowball" or "slushball" Earth, which maintained large areas of open ocean even at the glacial maxima (e.g., Kirschvink 1992, Hyde et al. 2000). The survival of diverse eukaryotic lineages is most consistent with the latter view, in which discontinuous ice cover provided numerous refugia for marine life (Runnegar 2000). Certainly, the presence of unequivocal fossils of crown groups of marine red, green, heterokont, and yellow-brown algae prior to 750 Ma implies that marine photosynthesis remained operative throughout the Sturtian, Marinoan, and Gaskiers glaciations. Early models suggesting that ice cover over a "hard snowball" Earth would be extremely thin and would readily permit photosynthesis have been replaced by more robust geophysical models that predict that ice thickness under these conditions would be far too great to support photosynthesis except in open-water refugia (Warren et al. 2002). Sealing the entire surface of the world's oceans would also quickly promote global oceanic anoxia and acidification, making respiration impossible and eliminating marine animals even if they lived in deep-sea vent communities. This combination of potential killing mechanisms that would affect both photosynthesizers and respirers implies that although the Neoproterozoic ice ages were probably the most severe glaciations ever experienced on Earth, it seems likely that "oases" of open water existed throughout these glacial episodes and provided refugia for marine eukaryotes, including early animals. Nonetheless, comparisons with the massive extinctions associated with less-severe Phanerozoic glaciations, such as the one at the end of the Ordovician (Brenchley et al. 1995), suggests that even "slushball" glaciations would have been evolutionary bottlenecks for life. The abrupt appearance of both large spiny acritarchs (Grey et al. 2003) and large Ediacara-type fronds (Narbonne & Gehling 2003) within 5 million years of the end of the Gaskiers glaciation implies that release of these stresses allowed eukaryotes to undergo an explosive diversification in the postglacial world.

The carbon-isotopic composition of sea water fluctuated in concert with these glaciations (Figure 1), with positive anomalies of up to +10‰ preceding each glaciation and negative excursions down to −5‰ accompanying each glaciation, perhaps reflecting the sequestering of organic carbon in the deep sea or in methane clathrates and then its abrupt release (Hoffman & Schrag 2002). Overall, carbon isotopes throughout the Cryogenian and Ediacaran are strongly positive (Figure 1), implying significant burial of organic carbon, perhaps owing to rapid burial of sediment during the dispersal of Rodinia (Kaufman et al. 1998). Large-scale burial of organic carbon implies a concomitant rise in oxygen (Derry et al. 1992), which has been recognized as a strict prerequisite of the origin of large Metazoa for more than 40 years (Nursall 1959). The oxygen threshold for the sustained development of complexly folded organisms, such as Cnidaria, or soft-bodied organisms with complex circulatory systems is estimated by various authors as being somewhere between 1%–10% of present atmospheric levels (Knoll & Holland 1994, Budd & Jensen 2000). It is possible that this essential threshold was achieved considerably earlier in Earth history, and that the diversification of large animals was then triggered by the release of other environmental stresses. However, evolutionary patterns evident through the terminal Neoproterozoic and Cambrian are also consistent with increasing oxygen through this interval (Runnegar 1991, Knoll 2003), implying that postglacial oxygenation may have been a trigger as well as a threshold factor in the appearance of large animals of the Ediacara biota.

EDIACARAN ASSEMBLAGES

Cluster analysis of the diverse fossils and localities that constitute the Ediacara biota worldwide (Waggoner 2003) has shown that most or all occurrences of Ediacara-type fossils can be grouped into three clusters:

- The Avalon Assemblage (Figure 2, see color insert) is the oldest (ca. 575–560 Ma; Benus 1988, Bowring et al. 2003) and occurs only in very deep-water, volcaniclastic settings of the Avalon Zone of Newfoundland (Misra 1969, Anderson & Conway Morris 1982, Clapham et al. 2003) and England (Ford 1958, Boynton & Ford 1995). Grazhdankin (2004) also included the much younger (<549 Ma), shallower (preserved in cratonic carbonates), and taxonomically very different (Waggoner 2003, figures 2 and 3) fossils of the Khatyspyt Formation of Siberia as part of the Avalon Assemblage, but this is not followed in the present review. The Avalon Assemblage is typified by rangeomorphs—bizarre frond-, spindle-, bush-, or comb-shaped colonies composed of highly fractal modular elements (Jenkins 1985, Narbonne 2004). None of the taxa were skeletonized or capable of mobility.

- The White Sea Assemblage (Figure 3, see color insert) is best known from the classic Vendian sections in the White Sea (Fedonkin 1981, 1992; Sokolov & Iwanowski 1990) and the Ediacara Member of Australia (Glaessner & Wade 1966, Jenkins 1992). The oldest occurrences are <560 Ma and the youngest may range to near the base of the Cambrian (Martin et al. 2000, Grazhdankin 2004). The most diverse assemblages lived in shallow-water settings between wave base and storm wave base and are characterized by segmented fossils, discoid fossils, and fronds. Abundant worm burrows attest to the presence of mobile bilaterians in the fauna, but none of the taxa were skeletonized. Lower diversity assemblages from mainly offshore and slope deposits in Finnmark (northern Norway), northwestern Canada, the Urals, and Khatyspyt in Siberia plot as a subassemblage in Waggoner's (2003, figure 2) analysis.
- The Nama Assemblage (Figure 4, see color insert) is best known from the Kuibis and Schwarzrand subgroups of the Nama Group in Namibia (Gürich 1933, Germs 1972, Narbonne et al. 1997, Grotzinger et al. 2000, Grazhdankin & Seilacher 2002). The type assemblage is of shallow-water origin and has been dated at >549–542 Ma (Grotzinger et al. 1995), although similar assemblages occur in both older and deeper-water strata elsewhere. The assemblage consists mainly of multifoliate fronds, bilaterian burrows, and early calcified metazoans.

The existence of these distinct Ediacaran assemblages has been widely accepted, but their interpretation remains controversial. Early attempts to regard these as reflecting biogeography are not supported by the lack of congruence between Ediacaran assemblages and known Ediacaran paleogeography (Waggoner 1999, 2003). A temporal influence is evident when the Khatyspyt Formation is properly assigned to the White Sea Assemblage (see above), with the Avalonian Assemblage predating all other assemblages (Waggoner 2003), but this apparent temporal control may equally well reflect a coincidental association of volcanism with the oldest known Ediacaran fossils. Grazhdankin (2004) demonstrated that White Sea– and Nama-type assemblages typified different environments in the succession in northern Russia and speculated that environment played a major role in controlling these assemblages worldwide, but a purely environmental control does not explain why deep-water Ediacaran assemblages from northwestern Canada (Narbonne & Aitken 1990) contain a White Sea rather than Avalonian Assemblage

(Waggoner 2003). The following section investigates the role of taphonomy as a factor influencing the nature and composition of Ediacaran assemblages.

PRESERVING THE EDIACARA BIOTA

Ediacara-type fossils almost exclusively represent soft-bodied organisms, most commonly preserved as impressions on the bases of sandstone beds. Virtually all Ediacara-type fossils are preserved as impressions on the bases of event beds, instantaneous deposits of sediment or volcanic ash on the sea bottom (Figure 5*a*,*b*, see color insert). Ediacara-type fossils typically exhibit high relief and lack carbonization or mineralization, and thus differ significantly from soft-bodied animals in Phanerozoic Lagerstätten (which are typically preserved as two-dimensional carbonized or mineralized films; Briggs 2003). This was taken by some authors as an indication that Ediacaran organisms were extremely firm-bodied (Seilacher 1989) or composed of woody rather than fleshy material (Retallack 1994), and phylogenetic models were then based on these interpretations. However, many Ediacara-type fossils appear to have been flexible with evidence of wrinkling (Gehling 1991, plate 2.2), overfolding (Seilacher 1992, figures 2 and 3), and ripping of delicate specimens (Runnegar & Fedonkin 1992, figure 7.5.7C), implying that they were mainly soft-bodied creatures.

Gehling (1999) argued that the high relief preservation of Australian occurrences of the Ediacara biota was made possible by molding of the nonmineralized organisms and colonies by microbial filaments to form a “death mask” that maintained the shape of the specimen and hastened lithification of the overlying bed. Subsequent studies have yielded additional evidence of a microbial role in preservation in the form of Ediacara-type fossils preserved on carbonaceous sheets and sheet-like intraclasts (Narbonne 1998, figure 10), traces of mat-grazing organisms (Seilacher 1999), and even preserved cyanobacterial filaments within the mat (Steiner & Reitner 2001). Gehling’s (1999) work clearly elucidates the important role of microbial mats in the preservation of the Ediacara biota and restores the view that Ediacara-type fossils represent mainly “soft-bodied” organisms and colonies.

A survey of Ediacaran ocurrences and fossils suggests that four distinct styles of preservation can be recognized:

- Flinders-style preservation (Figures 3*a*–*i* and 5*c*) exhibits a topologically complex surface, with impressions of the bases of holdfasts in the underlying mud (typically preserved as raised features on the bed soles), the tops of resistant epifaunal organisms such as *Dickinsonia* (Figure 5*c*) that were lying on the muds (typically preserved as negative features on soles), the bases of nonresistant epifaunal organisms such as frond “leaves” (typically preserved as positive impressions on soles), and abundant burrows (preserved in both positive and negative relief on bed soles). It is the characteristic mode of preservation of the most fossiliferous beds in the Ediacara Member in the

Flinders Ranges of Australia (Gehling 1999) and is also well described from the "interstratified sandstone and shale" facies of the White Sea (Grazhdankin 2004). Flinders-style preservation was best developed in shallow, sunlit environments between wave base and storm wave base, and it involved event deposition of storm beds on sea bottoms with a well-developed microbial mat. This lithified the sole of the overlying bed rapidly and, when a resistant organism/colony decayed, unlithified mud from the underlying bed moved upward to fill the impression of the organism/colony (Gehling 1999, figure 11). Less-resistant structures, such as frond leaves, were molded from beneath and cast by sand following decay of the organisms/colony, and structures that were partly buried in the substrate (frond holdfasts and burrows) were preserved when sand from the overlying event bed filled the open hole following departure/decay of the organism.

- Fermeuse-style preservation (Figures 3*j* and 5*a*,*d*) typically preserves only trace fossils and the bases of holdfasts. It is the characteristic mode of preservation in outer shelf and slope assemblages, such as the Fermeuse Formation of Newfoundland (Gehling et al. 2000), the Windermere Supergroup of northwestern Canada (Narbonne & Hofmann 1987, Narbonne & Aitken 1990), and the Innerelv Member of Finnmark in northern Norway (Farmer et al. 1992), and also may be responsible for beds with only discs and burrows in the otherwise richly fossiliferous sections at Ediacara and in the White Sea. It is herein hypothesized that the microbial mat was less developed than in Flinders-style preservation or that it consisted of heterotrophic or sulfur-oxidizing bacteria, which did not produce the rapid mineralization essential to lithify the sole of the overlying bed and preserve epifaunal organisms and colonies. Holdfasts and burrows were well preserved because they were partly buried in the substrate and thus did not require a microbial coating for preservation.
- Conception-style preservation (Figure 2*a*–*b*,*d*–*g*; 5*b*,*e*) preserves the organisms under a bed of volcanic ash to form an "Ediacaran Pompeii." It is the predominant mode of preservation in the Conception Group of Newfoundland (Seilacher 1992) and the Charnwood succession in England. Preservation began when volcanic ash instantaneously covered the organisms/colonies and molded their upper surfaces. Preservation of the tops of holdfasts and stems rather than their bases implies that lithification proceeded more rapidly in volcanic ash than in the sandstones of the Flinders-style preservation, presumably owing to early diagenesis of labile minerals in the ash. However, less resistant organic materials such as spindles collapsed or decomposed almost immediately, and the still-unlithified ash settled to preserve their impressions on the microbially coated deep-sea floor. Avalonian volcanic ashes weather recessively to reveal spectacular tennis-court-sized surfaces of silicified mudstone, each with the fossil impressions of the original biological community preserved in place on its upper surface (Figures 2*a* and 5*e*).

- Nama-style preservation (Figures 2*c*; 4*a*,*b*,*d*,*e*; 5*f*) preserves fossils as molds and three-dimensional casts within beds of storm- or turbidite-deposited sand, rather than at the base of the event bed as in the other three preservational modes. The best-known examples are from the Kuibis and Schwarzrand subgroups of Namibia in southern Africa that bear monospecific assemblages consisting of abundant *Pteridinium*, *Rangea*, *Ernietta*, or *Swartpuntia*; similar assemblages occur at isolated levels in Australia (Glaessner & Wade 1966), California/Nevada (Hagadorn & Waggoner 2000), the White Sea (Grazhdankin 2004), and Newfoundland (Narbonne 2004). Grazhdankin & Seilacher (2002) regarded these assemblages representing infaunal Ediacara-type organisms, but the unimodal orientation of the fossils in many of these occurrences implies that they lived epifaunally and were rapidly buried under the influence of a current or combined wave-current flow (Jenkins 1985, Narbonne et al. 1997, Narbonne 2004). Specimens in all of these deposits are preserved three dimensionally within the sandstone beds, with superb preservation of multifoliate structures not readily visible in Ediacara-type fossils preserved on bed soles (Figure 4*d*–*e*). There is no evidence of microbial molding of the fossils, and in some (perhaps all!) instances this has led to partial degradation of the exterior of the organisms/colonies to reveal resistant organic internal structures not seen in normal occurrences of the Ediacara biota (Dzik 1999; Narbonne 2004, figures 3B–D). As a consequence, the shape of the fossil in a within-bed preservation may have little resemblance to the external form of the original living organism (Dzik 1999). Most of the taxa typical of Nama-style preservation are reported only rarely from more "normal" preservations of the Ediacara biota, where they may be masquerading under different taxonomic names.

Owing largely to the preponderance of microbial mats and the scarcity of bioturbation in the Ediacaran, preservation of soft-bodied organisms and colonies was a normal event in many marine environments, and this is what makes Ediacaran paleobiology both possible and rewarding. However, there is no overlap between the features preserved in Fermeuse-style preservation (bases of discs), Conception-style preservation (upper surfaces of discs and lower surfaces of less-resistant organisms), and Nama-style preservation (three-dimensional casts of internal resistant structures within the organisms/colonies), and these differences in taphonomy can cause profound differences in the taxonomic composition of their preserved assemblages. It is as if event beds provided the taphonomic "camera" capable of recording the living assemblage as fossils, but that microbial mats, sediment, and volcanic ash provided three different types of "film" that were sensitive to very different wavelengths of light. For example, Ediacara-type fossils in the Drook, Briscal, and Mistaken Point formations of Newfoundland (Figure 6) are preserved as census populations on upper bedding surfaces beneath beds of volcanic ash (Conception-style preservation of a wide diversity of epifaunal organisms; Figures 2*a* and 5*b*,*e*), but the amount of volcanism in the area declined over

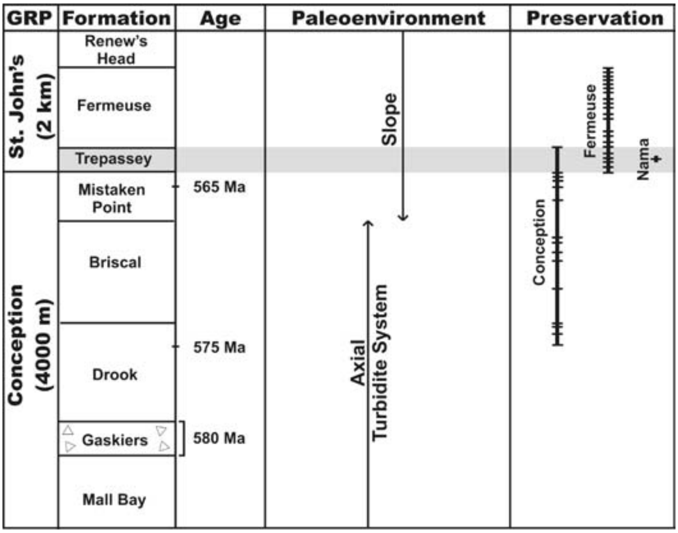

Figure 6 Stratigraphy of the Conception and St. John's groups in the Avalon Zone of Newfoundland showing U-Pb dates (Benus 1988, Bowring et al. 2003), depositional environments (Wood et al. 2003), and styles of fossil preservation (see text).

time and virtually all fossils in the Fermeuse Formation were specimens of the holdfast disc *Aspidella* preserved beneath sandy turbidites (Figure 5*d*). The intervening Trepassey Formation exhibits mainly Fermeuse-style preservation (Figure 6), but a volcanic bed near the top of the formation marks the last occurrence of Conception-style preservation of epifaunal fossils (*Charnia*, *Bradgatia*, and comb-shaped rangeomorphs), and a single bed of Nama-style preservation within a turbidite in the middle of the formation yields abundant specimens of typical Namibian genus *Rangea* (Narbonne 2004).

These preservational windows in the Trepassey Formation are difficult to explain as different communities. There are no obvious differences in environment in these uniform deep-water deposits (Wood et al. 2003), the different assemblages do not match observed succession in the Mistaken Point biota (Clapham et al. 2003), and where individual beds can be traced laterally for long distances there is no evidence of environmental patchiness or changes in their fossil assemblages (Clapham et al. 2003). There is no way that the living community could have known in advance whether it would be covered by volcanic ash (Conception-style preservation) or turbidites (Fermeuse-style preservation) or be incorporated within a turbidite (Nama-style preservation) so it could adjust its biological composition in advance of preservation. The most parsimonious explanation is that differential taphonomy was responsible for the taxonomic differences in these Ediacaran assemblages of the same age and environment. A similar situation may be seen in the shallow-water deposits of the White Sea (Grazhdankin 2004), where

Flinders-style preservation characterizes most of the succession except for the "interstratified sandstone" facies of the middle Verkhovka Formation, which contains Nama-style preservation and a Nama Assemblage of fossils including *Rangea*, *Pteridinium*, and *Swartpuntia*. It is intriguing to note that the Ediacaran assemblages identified by Waggoner (2003, figure 2), the Nama Assemblage, Avalon Assemblage, and two separate White Sea assemblages, each correspond to one of the four taphonomic styles for the Ediacara biota. This emphasizes that taphonomy exhibits a first-order control on the composition of Ediacaran assemblages worldwide. This will have minimal impact on sedimentological and ecological studies because taphonomy is commonly related to environmental parameters, but could significantly affect biostratigraphic and biogeographic analyses of the Ediacara biota.

AFFINITIES OF THE EDIACARA BIOTA

In a little more than a decade, the affinities of the Ediacara biota went from being a well-established "fact" to becoming one of the greatest controversies in paleontology. Early work on the affinities of the Ediacara biota was mostly by Australian workers, many of whom were superb invertebrate zoologists. Sprigg (1947, 1949) documented abundant discoid fossils at Ediacara that, on the basis of their circular shape and presence of radial and concentric markings (Figure 3*d*), he ascribed to fossil "jellyfish." In a series of publications spanning almost three decades and culminating with his two global syntheses, Glaessner (1979, 1984) expanded this view that Ediacaran taxa reflect crown groups of living phyla of marine animals: Fronds, such as *Charniodiscus* and *Charnia*, were regarded as pennatulacean Cnidaria; segmented fossils, such as *Dickinsonia* and *Spriggina*, were attributed to polychaete worms; and more complex segmented fossils were regarded as early trilobitomorph (*Vendia* and *Praecambridium*) and crustacean (*Parvancorina*) arthropods. His view that the Ediacara biota represents "the dawn of animal life" (Glaessner 1984), a biota characterized by jellyfish and frondose cnidarians with a few higher animals, dominated paleontological thought from the early 1960s until the mid-1980s.

This model was abruptly challenged by Seilacher (1984, 1989, 1992), who suggested that any similarities between Ediacara-type fossils and modern animals were either accidental or convergent, and that the Ediacara biota represents an extinct high-order taxonomic group—a "failed experiment" in the evolution of life. He argued that all Ediacara-type fossils were more similar to each other than to any living animals in being composed of an air-mattress-like construction of resistant "pneu" elements (Seilacher 1989), and that this pneu structure implied that the Ediacara biota should be classified as an extinct Kingdom of life, which he termed the Vendobionta (Seilacher 1992).

Seilacher's views provoked considerable controversy (Gehling 1991, Runnegar 1995). One immediate consequence was to turn the discussion of Ediacaran affinities from a monolith to a free-for-all, and in short order, the Ediacara biota had been reinterpreted as fossil protists (Zhuravlev 1993), lichens (Retallack 1994), extinct photosynthetic "metacellulars" (McMenamin 1998), prokaryotic colonies (Steiner & Reitner 2001), and fungi-like organisms (Peterson et al. 2003). It also stimulated research in comparative biology, taphonomy, and ecology in an attempt to deduce the affinities of these pivotal fossils in the evolution of life. Research in Ediacaran taphonomy showed that the organisms were composed of soft, flexible tissues and that there is no need to infer unusual compositions or biology for Ediacara-type fossils (Gehling 1999). Process-sedimentological studies of deep-water Ediacara-type fossils in northwestern Canada (Dalrymple & Narbonne 1996, MacNaughton et al. 2000) and Newfoundland (Wood et al. 2003) confirmed that the fossil organisms were untransported and lived in aphotic environments more than 1 km deep, and hence could not be photoautotrophs. Studies of the spatial distribution and community organization of the Mistaken Point biota showed that it is strikingly similar to that of modern communities of suspension-feeding animals (Clapham & Narbonne 2002, Clapham et al. 2003). The studies listed above imply that Ediacaran organisms most likely were animals or animal-grade organisms.

But what kinds of animals? Studies in comparative morphology and molecular biology provide critical clues to this question (Figure 7). The simplest and least-derived animal phyla are the radial phyla, the Porifera (sponges), and the Cnidaria (corals, jellyfish, sea anemones, etc.). Sponge biomarkers in Ediacaran hydrocarbons imply that sponges were abundant (McCaffrey et al. 1994), and this is spectacularly confirmed by fossils of the crown-group sponge *Palaeophragmodictyon*

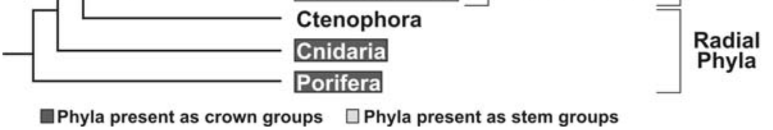

Figure 7 Molecular phylogeny of the animals, showing presumed evolutionary levels of the Ediacara biota. Phyla plausibly represented among the Ediacara biota are indicated; light shading where these fossils are represented by stem groups (ancestors lacking one or more diagnostic characters of the modern phylum), dark shading where fossils are represented by crown groups (ancestors exhibiting all of the diagnostic characters of the modern phylum) in addition to stem groups. Rangeomorphs (not shown) probably represent an extinct, phylum-level stem group of radial animals, perhaps intermediate between the Porifera and the Cnidaria. After Knoll & Carroll (1999).

(Figure 3*a*) from the Ediacaran of Australia (Gehling & Rigby 1996). Cnidaria also appear to have been present. *Charniodiscus* (Figure 3*e*) has long been considered as similar to modern soft corals, a view strongly supported by Conway Morris' (1993) description of *Thaumaptilon walcotti*, a Middle Cambrian Burgess Shale frond that resembles *Charniodiscus* but preserves probable zooids. More than half a century after Sprigg's original suggestion, and with many twists and turns in between, it still seems likely that the Ediacara biota was dominated by stem and crown groups of radial phyla (Porifera and Cnidaria).

Abundant trace fossils exhibiting structures typical of Phanerozoic and modern annelid and molluscan burrows (Narbonne & Aitken 1990, Jensen 2003) and Ediacara-type body fossils with bilateral symmetry and/or segmentation imply that bilaterians were an essential part of later Ediacaran ecosystems. Early work attempted to identify crown-group bilaterian phyla, but it now appears that few if any Ediacaran bilaterians had evolved all of the characters of their modern phyla and that most are better considered as stem groups, leading to the major bilaterian phyla and superphyla (Budd & Jensen 2000). Possible stem taxa of all three of the bilaterian "superphyla" (Figure 7)—the Ecdysozoa (e.g., *Spriggina*; Figure 3*c*), Lophotrochozoa (e.g., *Kimberella*; Figure 3*b*), and the Deuterostomata (e.g., *Arkarua*; Figure 3*h*)—have been recognized among the taxa of the Ediacara biota (e.g., Gehling 1987, 1991; Fedonkin & Waggoner 1997; Knoll & Carroll 1999).

Other Ediacaran taxa cannot easily be accommodated in existing animal groups. *Palaeopascichnus* and *Yelovichnus* (Figure 3*f*), formerly interpreted as meandering trace fossils, appear instead to represent serially repeated body fossils (Gehling et al. 2000), possibly giant protists (Seilacher et al. 2003). Even more intriguing, some Ediacara-type fossils may represent "failed experiments" at a high taxonomic level. The enigmatic fossil *Tribrachidium* (Figure 3*i*) has long been considered as distinct from modern organisms, although some workers have suggested affiliations with unusual sponges or the much smaller triradiate cones such as *Anabarites* that dominate early Cambrian assemblages of small shelly fossils. Multifoliate fronds such as *Pteridinium* and *Swartpuntia* have also proven difficult to relate to modern groups of organisms (Narbonne et al. 1997, Knoll 2003).

Perhaps the best example of an extinct high-level taxonomic group is that of the rangeomorphs (Jenkins 1985; synonymous with the "fractal serially quilted Vendobionta" of Seilacher 1992), a group of colonial organisms that exhibited a modular construction of similar, highly fractal elements (Narbonne 2004). These elements (Figure 2*c*) were combined as modules to construct frond-, spindle-, comb-, or bush-shaped colonies (Figure 2*a*,*b*,*d*–*g*) that filled most niches in the Mistaken Point ecosystem (Figure 2*h*). Rangeomorph communities are most similar to those of modern, suspension-feeding animals (Clapham & Narbonne 2002, Clapham et al. 2003), but it is difficult to relate rangeomorph morphology to any modern animals, and they appear to represent a "forgotten" architecture and construction that may represent an extinct phylum-level stem-group near the base of animal evolution (Figure 7). Rangeomorphs characterized the early stages of Ediacaran evolution, perhaps because their fractal growth and modular construction required less genetic complexity than was required by other animal phyla. Rangeomorphs were unable to compete with later, more highly evolved animals, and occur only rarely in younger Ediacaran assemblages and are not known from any Cambrian or younger assemblages including fossil Lagerstätten.

EDIACARAN EVOLUTION AND THE ORIGIN OF ANIMAL ECOSYSTEMS

Early Biological Complexity in the Deep Sea (575–560 Ma)

Precise U-Pb dates of zircons from volcanic ashes in eastern Newfoundland indicate that the Avalon Assemblage flourished 575–560 Ma (Figure 6) and is older than any other dated occurrence of Ediacara-type fossils (Martin et al. 2000). The Avalon Assemblage lived in a deep-water slope and basin floor environment that lacks evidence that either storm waves or light reached the sea floor (Wood et al. 2003). Microbial mats covered the sea floor, and contour currents were critical in bringing food and oxygen to these deep-sea communities. As with the earlier and simpler Twitya discs (Hofmann et al. 1990), shallow-water equivalents of the Avalon Assemblage have not yet been identified despite intensive search of appropriate strata worldwide, implying that the early evolution of the Ediacara biota may have occurred in predominantly deep-water settings.

The oldest known complex Ediacara-type fossils, indeed the oldest known large and architecturally complex fossils of any kind, occur in the upper beds of the Drook Formation (Narbonne & Gehling 2003) in strata that postdate the end of the Gaskiers glaciation by less than 5 million years (Bowring et al. 2003). Two species of the Ediacaran frond *Charnia*, *C. masoni* and *C. wardi* (Figure 2*f*), represent the most complex of the four species in the Drook Formation. These fronds reach lengths of nearly 2 m, the longest Ediacara-type fossils known, and exhibit differentiation into a holdfast and a frond with at least two scales of serial branching. Their large size, diversity, and architectural complexity implies that animals evolved before the Gaskiers glaciation and diversified in the postglacial world (Narbonne & Gehling 2003).

Approximately 30 taxa are known from the Avalon Assemblage in Newfoundland (Anderson & Conway Morris 1982), and a slightly younger assemblage containing some of these taxa is also known from Charnwood Forest in England (Boynton & Ford 1995). Most taxa of the Avalon Assemblage are strictly restricted to this assemblage. There is evidence of species-level biostratigraphy in the Avalon Assemblage, with some species of *Charniodiscus* (Laflamme et al. 2004), and spindles replaced upward by other species of the same genera despite similarity in facies. With the exception of the conical fossil *Thectardis* and the probable cnidarian frond *Charniodiscus*, most (>80%) of the distinctive taxa of Avalon Assemblage were rangeomorphs (Figure 2).

Conception-style preservation of untransported "census populations" of Ediacara-type fossils beneath beds of volcanic ash provides a unique opportunity to investigate Ediacaran community organization using modern methods in population and spatial ecology (Clapham & Narbonne 2002, Clapham et al. 2003). Bedding surfaces covered with untransported, current-aligned fossil fronds (e.g., Figure 2*a*) implies that these represent stalked epifaunal colonies that were tethered to the sea bottom and stood up above the sea floor (Seilacher 1992, 1999; Wood et al. 2003). Studies of epifaunal tiering (Clapham & Narbonne 2002), the development of a vertically stratified community structure above the sea bottom as a form of niche subdivision, showed three overlapping tiers (Figure 2*h*)—the absolute boundaries between tiers, percentage of organisms in each of these tiers, and maximum height of the highest tier are remarkably similar to those shown by modern and Phanerozoic communities of suspension-feeding animals (cf. Bottjer & Ausich 1986) and are quite unlike what is seen in tiering for light or other resources. Species richness, diversity, and single-species spatial patterns of the Mistaken Point communities are within the range of normal for modern epibenthic slope communities (Clapham et al. 2003). The inferred Mistaken Point succession, from high-dominance communities of low-level suspension feeders to more diverse and taxonomically even communities exhibiting complex tiering, is also similar to that inferred from modern and Phanerozoic marine communities (Clapham et al. 2003). These ecological similarities with modern communities, despite separation by more than half a billion years of animal evolution, imply that some key attributes of modern marine ecosystems were initiated during the earliest stages of animal evolution.

Other attributes of these earliest Ediacaran communities appear more primitive. There is no evidence of mobility among any of the preserved taxa—most were permanently attached to the sea bottom by a holdfast. There is no evidence for burrowing, infaunal tiering, macrophagous predation or scavenging, or macroscopic grazing on the microbial mat. Modern suspension-feeding patterns seem to have been established early in the evolution of animals, but more complex ecological interactions would have to wait for the advent of mobility and the acquisition of skeletal tools suitable for macropredation.

Acme of Ediacaran Form and Diversity (560–542 Ma)

Most of the latter half (560–542 Ma) of the evolution of the Ediacara biota is known mainly from shallow-water settings reflecting Flinders- and Nama-style preservation. With the exception of *Charniodiscus* and a few remaining rangeomorphs, these younger and shallower Ediacaran fossils are taxonomically very different from those of the Avalon Assemblage. Fossils are considerably more diverse at the generic level, and the difference in the diversity of body plans is even greater (Figures 3 and 4). Deep-water Ediacara-type fossils from western Canada are also of this age (Kaufman et al. 1998), but these occurrences comprise mainly Fermeuse-style preservation dominated by holdfast discs and trace fossils (Narbonne & Aitken 1990) with a single dickinsoniid in the uppermost (shallowest-water) strata (Narbonne 1994).

A critical innovation in younger Ediacaran assemblages was the appearance of megascopic bilaterians and bilaterian burrows (see Affinities of the Ediacara Biota, above). Their first appearance in shallow-water settings slightly more than

555 Ma is nearly coincident with the oldest representatives of the White Sea biota (Martin et al. 2000, Grazhdankin 2004) and thus may somewhat postdate their true evolutionary beginning. The oldest bilaterian burrows in deep-water deposits are in the Gametrail Formation of northwestern Canada (MacNaughton et al. 2000) in strata correlated chemostratigraphically with 550 Ma strata in Namibia. Many early bilaterians grazed on the microbial mat or burrowed within it, marking the beginning of the end of Precambrian-style ecosystems in which microbial mats covered all marine surfaces (Seilacher 1999).

The first calcified metazoans appeared 550 million years ago. Low-diversity assemblages of thinly calcified tubular (*Cloudina*) and goblet-shaped (*Namacalathus*; Figure 4*c*) animals appear in shallow-water carbonates worldwide. These taxa participated, along with calcimicrobes, in the construction of the first skeletal reefs in Earth history (Grotzinger et al. 2000, Hofmann & Mountjoy 2001). *Cloudina* tubes in the Dengying Formation of China show evidence that they were drilled by predatory organisms (Bengtson & Yue 1992, Hua et al. 2003)—the oldest evidence of macrophagous predation anywhere and a foreshadowing of the Phanerozoic world of tooth and claw that was about to unfold.

THE FATE OF THE EDIACARA BIOTA

Assemblages of Ediacara-type fossils continue to the Ediacaran-Cambrian boundary. In Namibia, abundant specimens of the multifoliate Ediacaran frond *Swartpuntia* (Figure 4*d*,*e*) are dated at $<543 \pm 1$ Ma, implying that they lived in the last one million years of the Proterozoic eon (Narbonne et al. 1997). However, the number of occurrences of Ediacaran "survivors" in the Cambrian can be counted on the fingers of one hand. Three hypotheses for the abrupt disappearance of Ediacara-type fossils may collectively explain this phenomenon.

Seilacher (1984) hypothesized that a mass extinction of the Ediacara biota in the late Neoproterozoic created an empty ecosystem into which the Cambrian biota radiated. Recent support for this idea comes from isotope chemostratigraphy (Figure 1), which records an exceedingly sharp C-isotope excursion to $-12‰$ that precisely marks the global extinction of *Cloudina* and *Namacalathus* and the position of the Ediacaran-Cambrian boundary (Amthor et al. 2003). This isotopic excursion may represent a short-lived interval of global anoxia (Kimura & Watanabe 2001) or widespread methane release.

The second focuses on changing taphonomic conditions across the Ediacaran-Cambrian boundary rather than an evolutionary disappearance of the Ediacara biota. Microbial mats are characteristic of most Proterozoic marine environments and were critical to the preservation of the Ediacara biota (Gehling 1999). The rapid evolution of grazing and burrowing organisms during the Cambrian explosion progressively restricted the environments in which microbial mats could form and be preserved, providing a taphonomic reason why Ediacara-type fossils should be rare in Cambrian strata (Jensen et al. 1998). This model explains why most of the few known Cambrian occurrences of the Ediacara biota exhibit Nama-style preservation (which does not depend on the presence of a microbial mat), but does not fully account for the extreme scarcity of Ediacara-type fossils in Lower Cambrian Lagerstätten, such as at Sirius Passet and Chengjiang.

A third explanation focuses on the ecological escalation brought on by the Cambrian "explosion" of animals. There is little evidence of macrophagous predation until near the end of the Ediacaran, but Early Cambrian communities show abundant evidence of Phanerozoic-style predation on soft-bodied and skeletal organisms (e.g., Bengtson 2002). The incoming of widespread predation appears to almost precisely coincide with the Ediacaran-Cambrian boundary, with the earliest Cambrian shelly fossil *Protohertzina* interpreted as representing the grasping spines of chaetognaths (Szaniawski 1982, 2002). The effects of introducing such predators into an Ediacaran biota in which most of the animals were immobile and nonskeletonized can readily be imagined. The resulting "evolutionary arms race" resulted in innovations in predation and defense, in burrowing for food and for shelter, and in the evolution of shells and brains. These features characterized the rapid diversification of the Cambrian explosion and led to the development of Phanerozoic and ultimately modern marine ecosystems.

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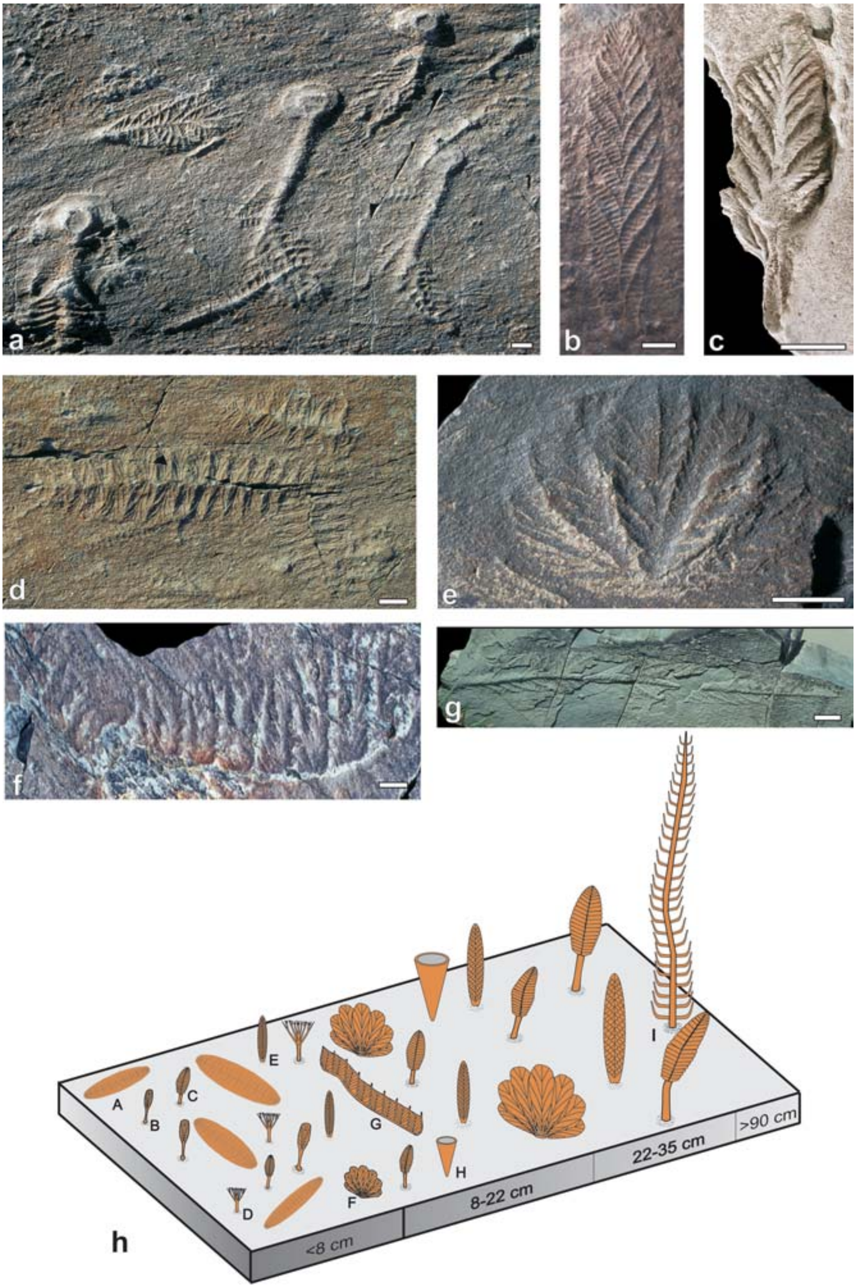

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Figure 2 Avalon Assemblage on upper bedding surfaces from Newfoundland (*a*, *c–h*) and Charnwood, England (*b*). Scale bar represents 2 cm (*a*, *b*; *d–g*) or 0.25 cm (*c*). (*a*) Current-aligned fronds of *Charniodiscus* (*lower and right-hand sides*), spindle-shaped rangeomorphs (*lower and center*), and a frond-shaped rangeomorph (*upper left*), Mistaken Point Formation. (*b*) Holotype of the probable rangeomorph frond *Charnia masoni*, New Walk Museum, Leicester. (*c*) Rangeomorph element showing three scales of fractal-like branching. Specimen exhibits Nama-style three-dimensional preservation. Trepassey Formation. After Narbonne (2004, figure 2A). (*d*) Spindle-shaped rangeomorphs, Mistaken Point Formation. (*e*) Bush-shaped rangeomorph (*Bradgatia*), Mistaken Point Formation. (*f*) Comb-shaped rangeomorph, with numerous linked frondlets sharing a common basal stolon, Mistaken Point. (*g*) Distal tip of the holotype of *Charnia wardi*, Drook Formation (Royal Ontario Museum 38628). (*h*) Diorama showing ecological tiering of Mistaken Point communities of the Ediacara biota. A: Spindle, B: Ostrich feather, C: *Charniodiscus*, D: Duster, E: *Charnia*, F: *Bradgatia*, G: Comb-shaped, H: *Thectardis*, I: Xmas tree. All except for C and H are rangeomorphs. After Clapham & Narbonne (2002).

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Figure 3 White Sea assemblage preserved on bed soles from Australia (*a–e*, *h–i*), northern Russia (*f* – *g*), and northwestern Canada (*j*). Images *a–c* courtesy of J.G. Gehling. See text for details of possible affinities. Scale bar represents 1 cm (*a–c*), 2 cm (*d*, *f–j*), or 5 cm (*e*). (*a*) *Palaeophragmodictyon*, a probable crown-group sponge, showing an osculum and a spicular net (South Australia Museum, P323332). (*b*) *Kimberella*, a possible stem-group mollusc. (*c*) *Spriggina*, a possible stem-group annelid or arthropod. (*d*) *Medusinites*, probably the holdfast disc of a frond (South Australia Museum, P13785-6). (*e*) *Charniodiscus*, a probable cnidarian (South Australia Museum, P19690). (*f*) Holotype of the serial fossil *Yelovichnus*, possibly a colonial alga or protist (Paleontological Institute, Moscow, 3993/1309). (*g*) The probable rangeomorph frond *Charnia* (Paleontological Institute, Moscow, 3993/1–15). (*h*) *Arkarua*, a possible stem-group echinoderm. (*i*) Holotype of *Tribrachidium*, a triradiate fossil of uncertain affinities (South Australia Museum, P12898). (*j*) *Helminthoidichnites*, a probable bilaterian burrow (Geological Survey of Canada 95924).

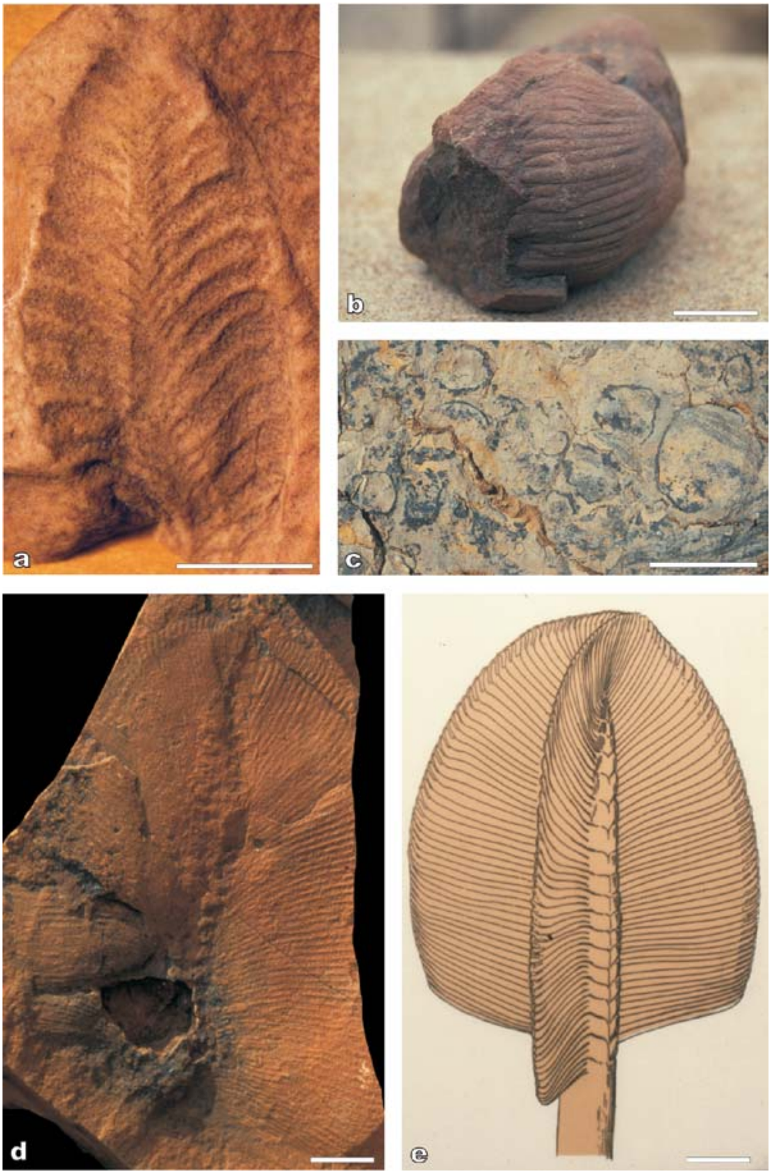

Figure 4 Nama Assemblage fossils from Nambia. Scale bar represents 2 cm. (*a*) Mold of the holotype of *Rangea*, a rangeomorph frond. (*b*) *Ernietta* preserved as a natural cast. (*c*) *Namacalathus*, a weakly calcified Ediacaran metazoan. (*d*, *e*) *Swartpuntia* holotype and reconstruction (after Narbonne et al. 1997) (Geological Survey of Namibia F238-H).

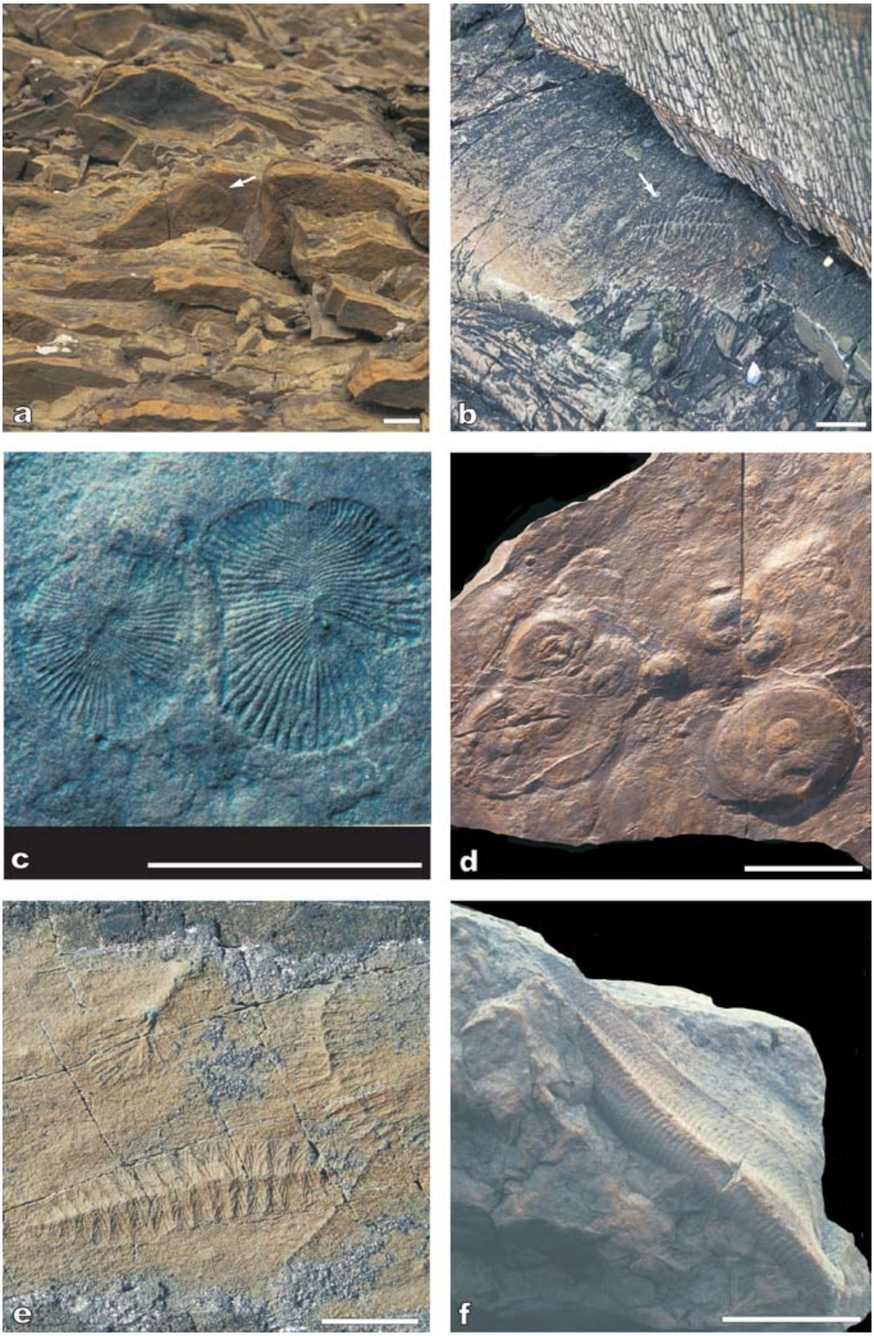

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Figure 5 Preservation of the Ediacara biota. The scale bar in all figures is 5 cm. (*a*) *Aspidella* (disc indicated with an *arrow*) preserved on the sole of a thin turbidite, Sheepbed Formation, northwestern Canada. (*b*) Spindle-shaped rangeomorphs (*arrow*) preserved on an upper bedding surface of silicified mudstone beneath a thick bed of volcanic ash, Mistaken Point, Newfoundland. (*c*) Flinders-style preservation of two specimens of *Dickinsonia* in negative relief on the sole of a storm sandstone from the Ediacara Member of Australia. Note the pustular nature of the surface, probably reflecting a microbial mat that covered the surface (South Australia Museum P13760). (*d*) Fermeuse-style preservation of abundant specimens of *Aspidella* on the sole of a turbidite sandstone from the Fermeuse Formation of Newfoundland (Geological Survey of Canada 116842). (*e*) Conception-style preservation of “spindles” and a “feather duster” in positive relief on an upper surface of the Mistaken Point Formation of Newfoundland. The surface is overlain by a thin bed of volcanic ash (*visible as dark bands at the top and bottom of the photograph and as the grey speckled grains between and even within the fossils*). (*f*) Nama-style preservation of a specimen of *Pteridinium* within a sandstone bed in the Kuibis Subgroup of Namibia.

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ERRATA

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