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## The Ediacara Biota: A Terminal Neoproterozoic Experiment in the Evolution of Life

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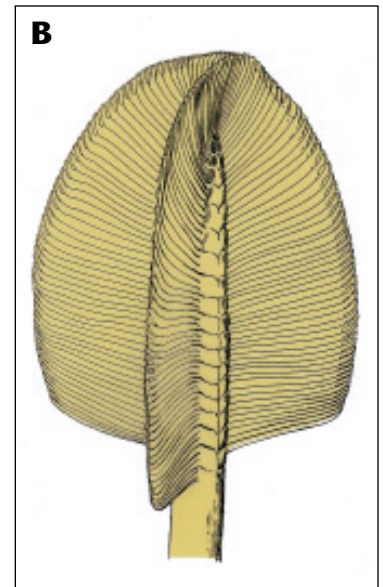
### ABSTRACT

The Ediacara biota is a distinctive assemblage of large, soft-bodied organisms that characterizes terminal Neoproterozoic (latest Precambrian) strata worldwide. Some Ediacaran organisms apparently were the root-stock for the Phanerozoic evolution of animals; other bizarre forms may represent a failed experiment in Precambrian evolution. The Ediacara biota and its nonactualistic preservation and ecosystem characterized the final 20 m.y. of the Proterozoic, and disappeared near the beginning of the Cambrian "explosion" of shelly and burrowing animals.

### INTRODUCTION

The terminal Neoproterozoic was a period of fundamental change in Earth history. Major changes included the breakup of the supercontinent Rodinia and the subsequent collision of some of the fragments that were to form Gondwana (Hoffman, 1992; Unrug, 1997), a succession of at least four global glaciations, and some of the largest known changes in the oceans and atmosphere (Knoll and Walter, 1992). It is against this backdrop that we see the appearance of abundant, large organisms, including the first definite fossil animals in Earth history, the Ediacara biota.

The Ediacara biota typifies terminal Neoproterozoic rocks worldwide (Glaessner, 1984; Fedonkin, 1992; Jenkins, 1992; Runnegar and Fedonkin, 1992). It was first described from Newfoundland and Namibia, but the name is derived from the superb assemblages of these fossils discovered at Ediacara in the Flinders Ranges of South Australia by Sprigg (1947). In contrast with the shelly fossils that characterize the Phanerozoic, the Ediacara biota consists almost exclusively of the remains of soft-bodied organisms, which are typically preserved as impressions on sand-



**Figure 1.** Photograph and artist's reconstruction of the holotype of *Swartpuntia gerssi* from Namibia. For simplicity, only three petaloids are shown. Metric scale. After Narbonne et al. (1997, Figs. 6 and 8).

stone beds (Fig. 1). The Ediacara biota contains a few forms that might be familiar to a modern beachcomber, alongside bizarre taxa whose place in the evolution of modern life is uncertain. A few "Ediacaran survivors" have been reported from the Cambrian, but most of the archetypal forms disappeared abruptly near the Cambrian "explosion" (Grotzinger et al., 1995). The unique biology, ecology, and preservational mode of the Ediacara biota effectively marks the end of the Proterozoic Eon, and may herald the beginning of the Phanerozoic.

### EVOLUTIONARY HISTORY

The Ediacara biota occupies a pivotal position in the evolution of life on Earth, between the largely microbial (especially stromatolitic) communities that characterize the classic "Precambrian" and the shelly biotas of the Cambrian and younger

Phanerozoic systems (cf. Sepkoski, 1981). Prior to the appearance of the Ediacara biota, Mesoproterozoic to mid-Neoproterozoic (1600–600 Ma) benthic communities had been dominated by prokaryotic microbes along with some sheetlike and ribbonlike algae (Knoll, 1992). Evidence from molecular phylogeny suggests that microscopic animals could have evolved sometime prior to the appearance of the Ediacara biota, but the exact timing remains debatable (Wray et al., 1996; Conway Morris, 1996). The oldest known megascopic Ediacara-type remains occur in the Twitya Formation of northwestern Canada (see Fig. 3, locality 22) immediately below tillites correlated with the Marinoan-Varanger glaciation and believed to be about 600 m.y. old (Hoffmann et al., 1990). The structures consist of centimeter-scale rings and discs that are

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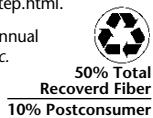
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Cockeysville, Maryland  
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**Frank A. Exum**  
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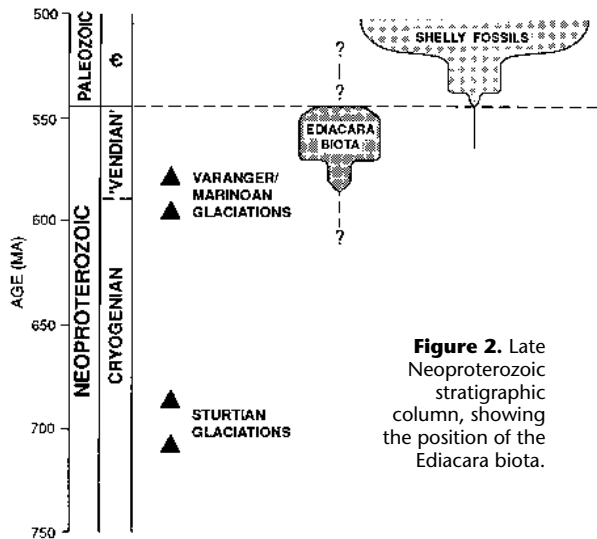
**Gus H. Goudarzi**  
*C. Ervin Brown*

**Ediacara Biota** *continued from p. 1*

similar to the simplest (most primitive?) elements of the Ediacara biota worldwide. A global rise in atmospheric oxygen in the Late Proterozoic may have been the trigger that permitted animals to achieve megascopic size at this time (Canfield and Teske, 1996).

Ediacaran biotas diversified rapidly after the end of the Neoproterozoic glaciations (Fig. 2) and are now known from some 30 localities on five continents, including at least seven distinct regions of

North America (Fig. 3). The known stratigraphic range of Ediacara-style biotas is approximately 55 m.y. (ca. 600–544 Ma), but diverse and complex fossils are known only from the final 20 m.y. of the Neoproterozoic (Fig. 2). At least three stratigraphically restricted assemblages have been recognized, each more diverse than its predecessor (Narbonne et al., 1994). It was formerly believed that the Ediacara biota disappeared several tens of millions of years before the beginning of the Cambrian, but precise U-Pb dates of fossiliferous strata in Namibia indicate that the



**Figure 2.** Late Neoproterozoic stratigraphic column, showing the position of the Ediacara biota.

Ediacara biota persisted to near the beginning of the Cambrian “explosion” (Grotzinger et al., 1995). Possible explanations for the abrupt disappearance of the Ediacara biota include elimination of a preservational “window” (Fedonkin, 1992), competition and predation by early skeletal animals (McMenamin, 1986), and global geochemical perturbations (Bartley et al., 1998).

## AFFINITIES

In a little more than a decade, the affinities of the Ediacara biota have gone from being a well-documented “fact” to becoming one of the great controversies in paleobiology. Prior to the mid-1980s, virtually all workers emphasized similarities in two-dimensional structure between Ediacaran fossils and living groups of jellyfish, soft corals, annelid worms, and arthropods, and concluded that the Ediacara biota represented the direct ancestors of these modern groups. Glaessner (1984) aptly termed this “The dawn of animal life.” In contrast, Seilacher (1982, 1989, 1992) believed that most of the Ediacara biota was unrelated to modern organisms, a “failed experiment” in the history of life on Earth. Seilacher suggested that Ediacaran organisms be referred to his new phylum or kingdom “Vendozoa,” which consists of quilted organisms that lacked mouths and guts and received energy by absorbing dissolved organic molecules or by harboring photosynthetic or chemosynthetic symbionts. The rival classifications of Glaessner and Seilacher represent two end-member views that have generated lively debate in the literature over the past decade (Gehling, 1991; Runnegar, 1995). Seilacher (1992) subsequently restricted his original concept of the “Vendozoa” (which he now terms the “Vendobionta”) and specifically removed taxa that he now regards as true animals.

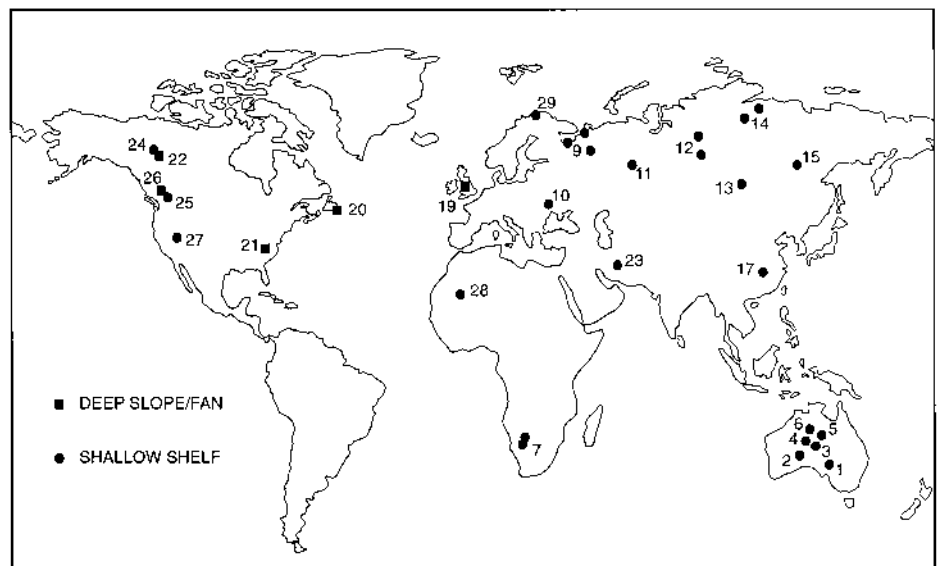
In my view, any interpretation that unites the disparate fossils of the Ediacara biota into a single taxonomic group, be it jellyfish, protists, lichens, or vandozoans, should be viewed with suspicion. Ediacaran fossils range from centimeter-scale blobs to complexly segmented discs and fronds more than 1 m long. Symmetry ranges from bilateral to trigonal to tetragonal to pentamerous to radial. Some were soft and jellylike; others were highly resistant to both mechanical stress and decomposition. Different taxa lived under conditions ranging from shallow, sunlit shelves to the deep seafloor. Several distinct groups can be recognized; I focus here on the three most common and familiar.

The least equivocal are the trace fossils, which are represented almost exclusively by simple subhorizontal burrows (Fig. 4). These show evidence of mobility and imply concentration of sensory organs at a “head” region. All previous workers have regarded these simple trace fossils as the work of bilaterian animals (e.g., Seilacher, 1989; Narbonne and

Aitken, 1990; Fedonkin and Runnegar, 1992).

The second are the nonresistant “discs” such as *Ediacaria* and *Cyclomedusa* (Fig. 5). These were originally interpreted as jellyfish (medusoids), but considerations of the morphology and preservation of these discs have progressively eliminated taxa to the point that no undoubted “jellyfish” remain among the Ediacara biota! All appear to have been bottom-dwelling (benthic) organisms, and many seem to have been permanently attached to the sea bottom (Seilacher, 1982; Narbonne and Aitken, 1990; Gehling, 1991; Fedonkin and Waggoner, 1997). The centimeter-scale disc to hemisphere *Beltanelliformis* (Fig. 6), perhaps the most common and widely distributed Ediacaran fossil worldwide, is strikingly similar to the base of some anemones and especially to the bases of Paleozoic burrows generally attributed to anemones (Narbonne and Hofmann, 1987; Fedonkin and Runnegar, 1992). Larger discs such as *Ediacaria*, some of which are as large as a dinner plate, are more controversial. Most show no evidence as to the nature of their upper surface, but several taxa show evidence of hairlike markings extending radially from a central disc (e.g., Fig. 5A) which might alternatively be regarded as the tentacles of a polyp or the rootlike structures of a

**Ediacara Biota** continued on p. 4



**Figure 3.** Global distribution of principal Ediacara-type fossil assemblages and environments. Data from Glaessner (1984, Fig. 1.8, localities 1–23), Hofmann (1987, Fig. 13, localities 24–25) and recent literature (localities 26–29). Glaessner’s localities 8 (calcareous tubes), 16 (pseudofossils), and 18 (Cambrian) have been omitted, as have several low-diversity assemblages of discs and problematica described subsequently. Australia: 1—Flinders Ranges, Adelaide “Geosyncline”; 2—Officer Basin; 3 and 4—Amadeus Basin; 5—Mt. Skinner; 6—Georgina Basin. Africa: 7—Namibia; 28—Algeria (Bertrand-Sarfati et al., 1995). Europe: 9—White Sea, Russia; 10—Podolia, Ukraine; 11—Urals; 19—Charnwood Forest, England; 29—Finnmark, Norway (Farmer et al., 1992). Asia: 12—Yenisey River, Siberia; 13—Lake Baikal, Siberia; 14—Anabar and Olenok, Siberia; 15—River Maya, Siberia; 17—Yangtze Gorge, China; 23—Iran. North America: 20—Avalon Peninsula of Newfoundland; 21—North Carolina; 22—Mackenzie Mountains, northwestern Canada; 24—Wernecke Mountains, northwestern Canada; 25—Rocky Mountains, British Columbia; 26—Cariboo Mountains, British Columbia (Ferguson and Simony, 1991); 27—Spring Range, Nevada (Horodyski, 1991; Waggoner and Hagadorn, 1997).



**Figure 4.** Simple burrows following a carbonaceous layer in the Wernecke Mountains, northwestern Canada. Scale in millimeters. After Narbonne and Hofmann (1987, Fig. 10a).

### Ediacara Biota continued from p. 3

holdfast (Runnegar, 1995). Others are attached to tubelike structures (Fig. 5B) or even complete fronds (Jenkins, 1992), and are best interpreted as holdfasts.

A third group are potential true Vendobionta (sensu Seilacher, 1992). Seilacher (1989, 1992) has shown that their distinctive quilted structure (Figs. 1, 7) is constructed of parallel, linked tubular segments in which the walls were more resistant than the ceilings. After the organism died, segments could become deflated or even imbricated. These organisms were formerly regarded as representing the ancestors of several modern groups ranging from soft corals to annelid worms (Glaessner, 1984). However, close similarity of the quilted constructional elements among architectures that range from erect multifoliate “fronds” (e.g., *Swartpuntia*; Fig. 1) to flat reclining sheets (e.g., *Dickinsonia*; Fig. 7A) implies that these taxa were more similar to each other than to any modern organisms (Narbonne et al., 1997). The Vendobionta appears to be a distinctive clade (monophyletic group) of Neoproterozoic organisms, but its taxonomic position is uncertain; suggestions range from an extinct group within the phylum Cnidaria (which also includes modern corals and anemones) to an extinct phylum or even kingdom unrelated to the subsequent Phanerozoic evolution of animals (Buss and Seilacher, 1994).

### PRESERVATION

If almost all Ediacaran organisms were soft-bodied, how were they preserved so abundantly worldwide? First and foremost, Ediacara-type fossils are preserved in event beds. These soft-bodied organisms lived on the mud bottom, and their impressions were preserved when they were catastrophically covered by a bed of sand-sized debris (an event). One famous example is the felsic tuff that covers the fossil surface at Mistaken Point in Newfoundland (Fig. 8A). This tuff has been



**Figure 5.** Ediacaran discs from northwestern Canada. Scale in millimeters. **A:** *Hiemalora* from the Mackenzie Mountains. Note pustular surface with carbonaceous coating, and radiating tentacle-like markings to left. After Narbonne (1994, Fig. 3.1). **B:** *Ediacaria (Beltanella)* with overlying stem (right side of disc) from the Mackenzie Mountains. After Narbonne and Aitken (1990, Pl. 1, Fig. 1).

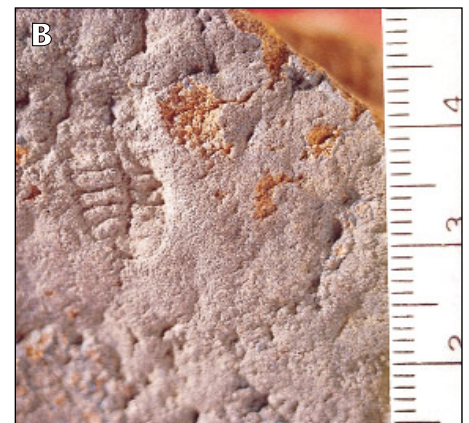
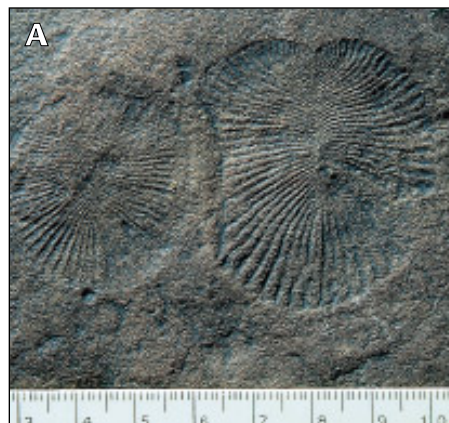


**Figure 6.** The probable anemone *Beltanelliformis* from the Bernashev Member, Ukraine. Metric scale.

dated at  $565 \pm 3$  Ma (U-Pb on zircons; Benus, in Landing et al., 1988), providing a precise date for this “Ediacaran Pompeii.” The most common mode of preservation of the Ediacara biota worldwide is on the soles of storm or turbidite beds (Fig. 8B), again reflecting instantaneous deposition of sand on the muddy seafloor. Wade (1968) recognized two preservational modes that reflected resistance to decomposition. In particular, most discs decomposed prior to cementation of the

overlying sand bed and thus are preserved as ridges on its sole (Figs. 5, 6), whereas most quilted fossils (e.g., *Dickinsonia*) did not decompose until after cementation of the sand and are preserved as indentations on the base of the bed (Fig. 7). Resistant organisms can even be preserved within and on top of storm beds (Fig. 9), but this is extremely unusual for nonresistant discs.

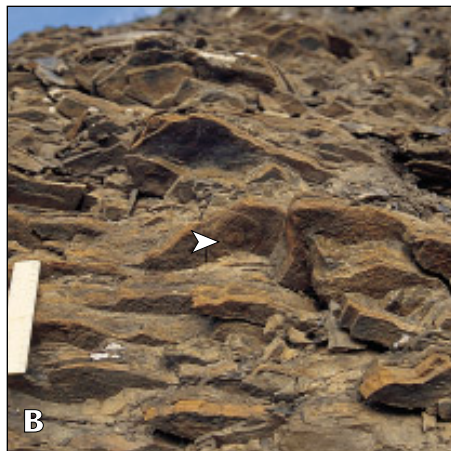
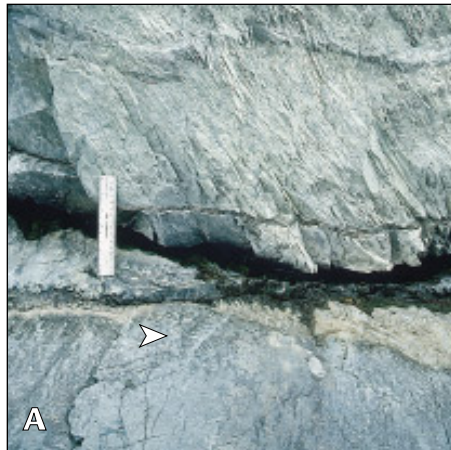
One might expect exquisite preservation of soft organisms under a layer of submarine volcanic ash such as at Mistaken Point, but why do some thick storm deposits and proximal turbidites faithfully preserve delicate structures on Ediacaran fossils despite the obvious evidence of high-energy conditions during deposition? The answer seems to lie in the warty, pustular texture that marks most fossiliferous Ediacaran surfaces (Figs. 4–7). Russian paleontologists refer to this as “old elephant skin,” and it provides the search image for Ediacaran fossils on at least three continents; it is rarely found in beds that do not contain Ediacaran fossils, and these fossils are almost never found in beds that lack this texture. Gehling (1987)



**Figure 7.** Dickinsoniids preserved as indentations on bed soles from Ediacara, Australia (A), and the Mackenzie Mountains, northwestern Canada (B). Metric scale. **A:** Two specimens of *Dickinsonia costata*. South Australia Museum P13760. **B:** *Windermeria aitkeni*. After Narbonne (1994, Fig. 3.2).

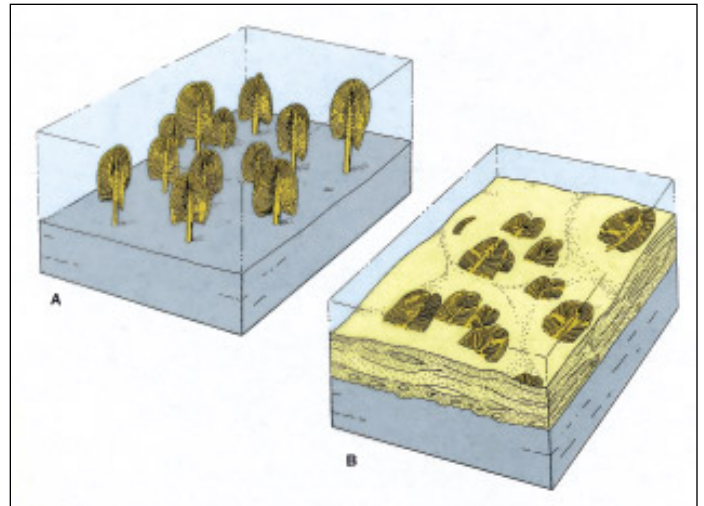
first recognized the similarity between these surfaces and modern microbial mats and has concluded that these mats were instrumental in stabilizing the mud surface and perhaps providing a “death mask” on the organism itself. In most cases, the distinctive texture is all that remains of the former microbial mat, but in northwestern Canada mats are preserved as black carbonaceous sheets that coat the fossil surfaces and that are locally ripped up to form intraformational conglomerates of carbonaceous sheets, some still bearing fossil impressions (Fig. 10).

The prevalence of microbial mats throughout the subtidal realm represents a nonactualistic feature of Neoproterozoic seas (Seilacher and Pfluger, 1994; MacNaughton et al., 1997). Bioturbation, cropping, and competition resulted in severe reduction of these mats in the Early Cambrian and, thus, less likelihood of preserving soft-bodied organisms on sandstone soles. However, with a few notable exceptions (see e.g., Conway Morris, 1993), complex Ediacara-type organisms are also absent from Cambrian Lagerstätten such



**Figure 8.** Preservation of Ediacaran fossils in North America. Arrows show their positions. Ruler is 15 cm long. **A:** Felsic tuff ( $565 \pm 3$  Ma) covering the fossil surface at Mistaken Point, Newfoundland. **B:** *Cyclomedusa plana* on sole of a turbidite in the Sheepbed Formation at Sekwi Brook, northwestern Canada.

**Figure 9.** Living assemblage (A) and preservation (B) of *Swartpuntia germsi* from Namibia. Specimens lived on the mud bottom and are preserved within and on top of the bed of hummocky cross-bedded sandstone. After Narbonne et al. (1997, Fig. 11).



as the Burgess Shale, implying that the disappearance of the Ediacara biota was not solely preservational.

## ECOLOGY

As discussed above, recent studies suggest that the Ediacara biota consists mainly of benthic organisms, most of which are in their original life position. Shallow-water deposition characterizes the vast majority of Ediacaran fossil sites (Fig. 3), including the classic sites in Australia, Namibia, and northern Russia (Gehling, 1988; Narbonne et al., 1997; Grazhdankin and Ivantsov, 1996). Fossiliferous sandstones in all these regions contain wave ripples and hummocky cross-stratification, but they typically lack true desiccation cracks and other evidences of emergence. Most fossiliferous strata were deposited between wave-base and storm wave-base, and were probably within the euphotic (photosynthetic) zone. A handful of deep-water occurrences of the Ediacara biota are also known (Fig. 3), principally in the Avalon Zone of eastern North America and England (Jenkins, 1992). Shallow-water features have not been found in any of these successions, and process sedimentology studies (such as those carried out at Mistaken Point in Newfoundland; Landing et al., 1988) imply that the strata were deposited on a deep-sea turbidite fan, but the subsequent tectonic history of these regions makes calculations of absolute depth impossible. Diversity is moderate to high, but only one taxon (*Charnia*) from Mistaken Point and Charnwood Forest is also known from shallow-water successions. However, it is uncertain whether the unusual composition of these assemblages reflects the deep-water setting or paleogeographic isolation of the terminal Neoproterozoic.

The Windermere Supergroup of northwestern Canada provides a unique natural laboratory to study the depth distribution of the Ediacara biota on a single



**Figure 10.** Conglomerate of carbonaceous rip-up clasts, with a specimen of *Spriggia* preserved on a clast, from the Wernecke Mountains of northwestern Canada. GSC 83030.

lithospheric plate. Strata were deposited in shelf and slope settings on the margin of the opening proto-Pacific Ocean. Shelf facies in the Wernecke Mountains comprise mainly storm-deposited sandstones that were laid down in shallow, wave-agitated, and probably euphotic environments (Narbonne and Hofmann, 1987). In contrast, slope facies in the Mackenzie Mountains lack shallow-water features and are characterized by turbidites, contourites, and mass-flow deposits that accumulated in 1.0–1.5 km water depth on the continental slope (Dalrymple and Narbonne, 1996). Ediacara-type fossils in both regions appear to be in their original life positions. The principal difference in biota between these two environmental regimes is the extreme abundance of probable anemone *Beltanelliformis* in the shallow-water assemblages of the Wernecke Mountains and its complete absence from the deep-water assemblages in the nearby Mackenzie Mountains. This mirrors global trends—*Beltanelliformis* occurs profusely in shallow-water settings worldwide but has not yet been found in any deep-water succession. Few other differences in composition are evident, suggesting that the

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## Ediacara Biota continued from p. 5

depth-related zonations that characterize Phanerozoic and modern seas were not strongly developed in the terminal Neoproterozoic (Narbonne and Aitken, 1990).

In some ways, the Ediacaran ecosystem differed significantly from all modern systems. Microbial mats covered most marine surfaces and exerted a major influence on sedimentation patterns. Burrowing organisms were sparse and mostly ineffective bioturbators, and no animals seem to have been capable of preying on the largely soft-bodied and immobile Ediacaran organisms. McMenamin (1986) has referred to this as "The garden of Ediacara," and in many ways it reflects the last vestiges of the Precambrian lifestyle that had characterized the preceding 3 b.y. of Earth history. However, the presence of anemones (Gehling, 1988) and sponges (Gehling and Rigby, 1996) among the Ediacara biota implies that ecological niches in the Ediacaran seas included microcarnivores and filter feeders. Ecological tiering included, for the first time, three feeding levels: an elevated level in the water column occupied by the fronds; a seafloor level with anemones, sponges, and a variety of other organisms; and the shallow subsurface where wormlike bilateria burrowed beneath microbial mats. These ecological innovations laid the groundwork for the massive ecological changes of the Cambrian "explosion," and thus marked the beginning of our Phanerozoic world.

## ACKNOWLEDGMENTS

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