EXCEPTIONAL FOSSIL PRESERVATION: A Unique View on the Evolution of Marine Life

Edited by
DAVID J. BOTTJER

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A Unique View on the Evolution of Marine Life

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Enigmatic Ediacara Fossils: Ancestors or Aliens?

David J. Bottjer

THE EDIACARA FOSSILS, OF LATE PRECAMBRIAN (VENDIAN) through Cambrian age, are among the most remarkable fossil biotas known from the stratigraphic record. This stems from the fact that this biota is thought to include fossils of some of the earliest larger organisms, whose nature has been much debated: Are they ancient representatives of still extant metazoan phyla, do they represent phyla or a kingdom now extinct on Earth, or could they even be colonial procaryotes or fossil lichens? Furthermore, when compared with younger deposits, this biota is in general a taphonomic anomaly. The Ediacara fossils represent remains of completely soft-bodied organisms, and yet they are commonly preserved in coarser-grained siliciclastics deposited in relatively well oxygenated marine environments, a seemingly improbable phenomenon not known elsewhere from the marine fossil record. Because Ediacara fossil preservation is commonly associated with some sort of event bed, varying from tidal sandstones to storm beds, to turbidites and subaqueous ash falls, their taphonomic context is best thought of as obrution deposits.

Fossils we now recognize as Ediacara were discovered as early as the nineteenth century in England at the Charnwood Forest locality (Hill and Bonney 1877) and in the early twentieth century in Namibia (Gürich 1930). However, their importance was not internationally recognized until the 1940s when R. C. Sprigg, an assistant government geologist of South Australia, discovered fossils of late Precambrian soft-bodied organisms in the Ediacara Hills of the Flinders Range, 600 km north of Adelaide. Sprigg's (1947, 1949) discoveries led to the extensive work of Glaessner (1961, 1969, 1983, 1984; Glaessner and Wade 1966) and

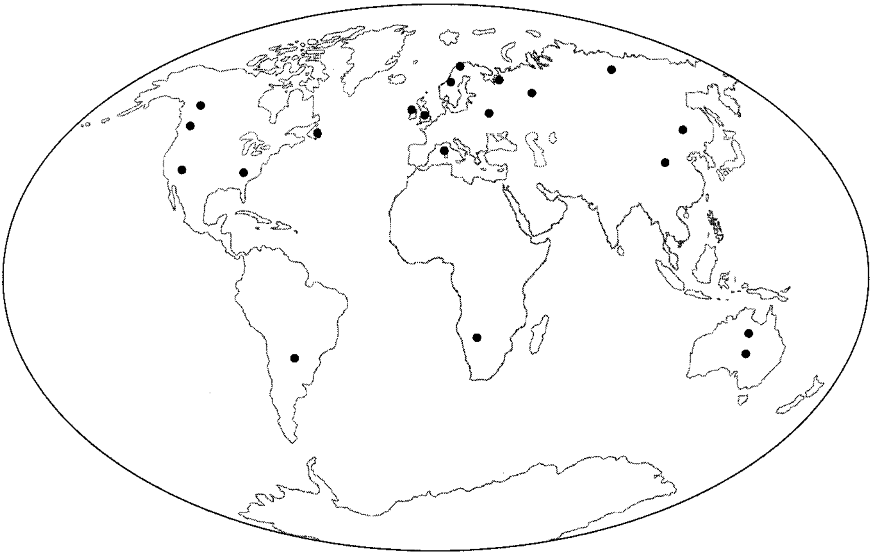

FIGURE 2.1 Global location, marked by dots, of the Ediacara biota; see text for indicated sites.

Wade (1972a, 1972b), who systematically documented this fauna and its preservation. This work in South Australia led to the appellation "Ediacara fauna" and fostered recognition that these fossils of soft-bodied organisms correspond to those in Charnwood Forest and Namibia and have a worldwide distribution, with other occurrences including the United States (California, Nevada, North Carolina), Canada (British Columbia, Yukon, Northwest Territories, Newfoundland), South America, Wales, Ireland, Sardinia, Norway, Finnmark, Russia (White Sea area, Urals, Siberia), Ukraine, central Australia, and China (Liao-Dun Peninsula, Heilongjiang Province, Yangtze Gorges) (Fedonkin 1992; Waggoner 1999) (Figure 2.1). The entire Ediacara biota was once thought to have become extinct well before the beginning of the Cambrian, but recent research indicates that at least portions of this biota survived into the Cambrian (Conway Morris 1993; Crimes, Insole, and Williams 1995; Grotzinger et al. 1995; Jensen, Gehling, and Droser 1998; Hagadorn, Fedo, and Waggoner 2000).

GEOLOGICAL CONTEXT

Among the numerous localities where Ediacara fossils are found, paleoenvironmental reconstructions indicate that these organisms lived in a variety of shallow- to deep-marine environments (Conway Morris 1990; Narbonne and Aitken 1990; Runnegar 1992; Seilacher 1992; Crimes, Insole, and Williams 1995; Narbonne 1998). Detailed accounts in this chapter will concentrate on two examples: the Flinders Ranges fauna, which is interpreted to have lived in nearshore to shallow shelf environments, and the fauna found on the Avalon Peninsula of Newfoundland, which has been interpreted as deep marine in origin (Gehling 1999; Narbonne, Dalrymple, and Gehling 2001; Wood et al. 2001).

Folded and faulted outcrops of upper Proterozoic strata occur discontinuously in the Flinders Ranges (Figure 2.2). Ediacara fossils are found in the Ediacara Member of the Rawnsley Quartzite (Pound Subgroup), which occurs in a thick sequence of sedimentary rocks of late Proterozoic age (Figure 2.3). The Pound Subgroup is overlain by Cambrian strata with definite Cambrian trace fossils, although the exact

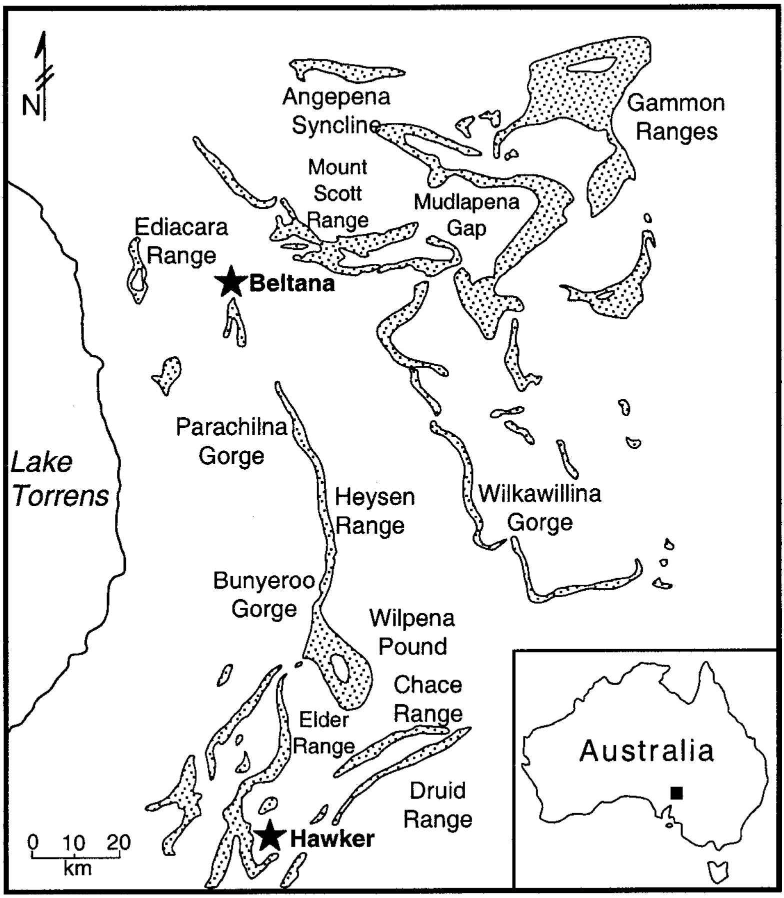

FIGURE 2.2 Generalized geologic map of the Flinders Ranges in South Australia illustrating the distribution of the upper Proterozoic Pound Subgroup (stippled). (Modified from Mount 1989)

relationships at the contact are of considerable controversy (Mount 1989, 1991; Nedin and Jenkins 1991).

Upper Proterozoic rocks are a prominent component of the Avalon Peninsula in Newfoundland, and the Mistaken Point area represents a classic locality for Ediacara fossils (Figure 2.4). Ediacara fossils from the Avalon Peninsula are found in the upper part of the Conception Group (Briscal and Mistaken Point Formations) and the overlying lower part of the St. John's Group (Trepassey and Fermeuse Formations) (Figure 2.5). The stratigraphic interval that bears Ediacara fossils contains mainly deep-marine slope turbidites with interbedded graded ash layers (Narbonne, Dalrymple, and Gehling 2001; Wood et al. 2001). In the Mistaken Point Formation, there is a tuff band that has been dated at 565 ± 3 my (Benus 1988).

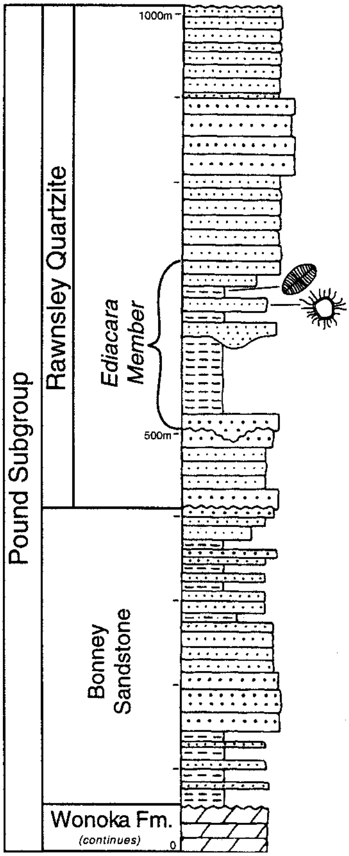

FIGURE 2.3 Generalized, composite stratigraphic column for the upper Proterozoic Pound Subgroup of the Flinders Ranges in South Australia; thicknesses and lithostratigraphy are approximate. The stratigraphic interval that contains the Ediacara biota is indicated by schematic fossils. (Modified from Mount 1989)

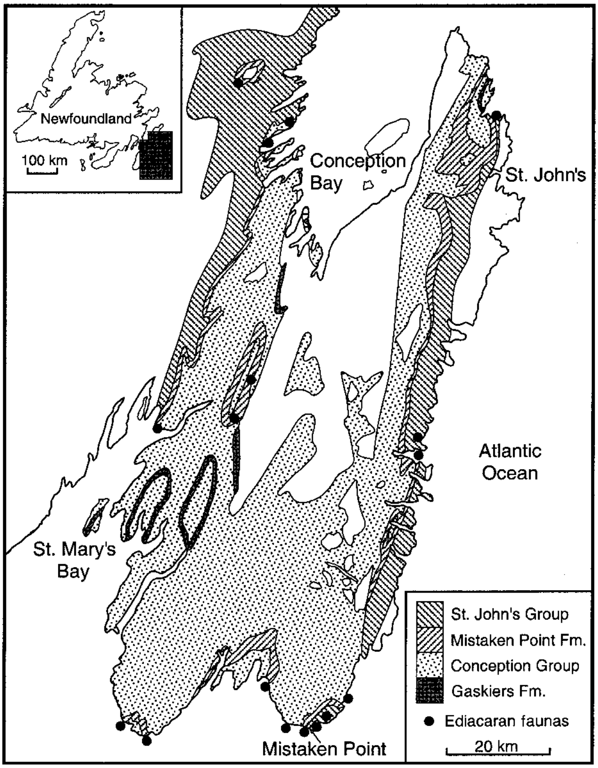

FIGURE 2.4 Generalized geologic map of the Avalon Peninsula in southeastern Newfoundland showing the distribution of upper Proterozoic St. John's Group and Conception Group (which includes the Mistaken Point and Gaskiers Formations) and of sites at which Ediacara faunas are found. (Modified from Jenkins 1992)

PALEOENVIRONMENTAL SETTING

The Rawnsley Quartzite contains thick, clean feldspathic sandstones that Gehling (1982, 1983, 1999) and Jenkins, Ford, and Gehling (1983) have interpreted as having accumulated in an environmental gradient ranging from shallow marine to intertidal sand flats. A sequence of thin, wavy-bedded sandstones; massive, channelized sandstones; and siltstones is found in the Rawnsley Quartzite in the central and southern Flinders Ranges (Mount 1989). The wavy-bedded sandstone interval is the lithofacies in which the Ediacara fossils are found, and this has been termed the Ediacara Member (Figure 2.3). Fossils are found only on the soles of flaggy sandstone beds (Glaessner 1984).

A number of sedimentological studies have been made of the flaggy sandstones of the Ediacara Member. Sprigg (1947) originally postulated that organisms of the Ediacara soft-bodied fauna were preserved on intertidal flats or along the strandline. Deposition in a tidally influenced

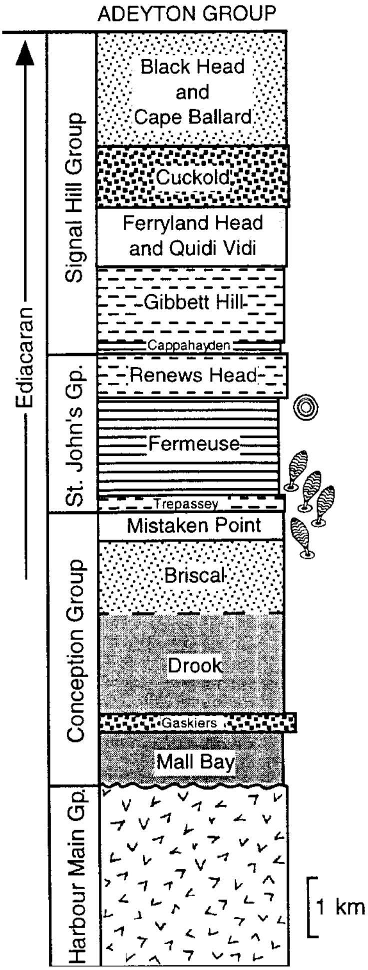

FIGURE 2.5 Generalized stratigraphic column for the upper Proterozoic of the Avalon Peninsula, Newfoundland, with stratigraphic intervals where Ediacara faunas are found indicated by schematic fossils. (Modified from Jenkins 1992)

environment was also supported by the studies of Glaessner (1961) and Jenkins, Ford, and Gehling (1983). However, Goldring and Curnow (1967) made a detailed study of the fossiliferous interval and interpreted it as having been deposited in an offshore neritic environment. Similarly, Gehling (1982, 1983, 1999) has concluded that the upper fossiliferous portion of the Ediacara Member (Figure 2.3) represents shallow subtidal, storm-dominated shelf sandstones and siltstones (Mount 1991). Thus, the most likely interpretation for the origin of the flaggy sandstone beds is that they are of storm origin.

Seilacher (1989) has observed that although many of the thinner sandstone beds show various characteristics of storm beds (grading of grain sizes and bedforms, oscillation-rippled tops), their soles lack the tool marks and other erosional features that are usually characteristic of Phanerozoic storm beds. Seilacher (1989) has also noted that when these sandstone beds directly overlie each other, soles mold the ripple marks of the underlying bed without any of the erosion typically found in storm beds. This variety of evidence thus led him to conclude that the sands were covered with extensive cyanobacterial mats that inhibited erosion. In the Ediacara Member, Seilacher (1989) also observed flat pebbles of coarse sand that were bent like a piece of leather during transport, and concluded that this is further evidence for the presence of extensive mats. The presence of these microbial mats very likely strongly influenced the preservation of these Ediacara fossils (Gehling 1986, 1999).

In Newfoundland, turbidites in the Mistaken Point Formation are relatively fine-grained (Landing et al. 1988; Jenkins 1992). In the Mistaken Point area (Figure 2.4), which is a well-known fossil site, these turbidites (thicknesses ranging from 10 to 80 cm) thicken and thin over a vertical distance of 6 to 8 m and were deposited in a deep-marine, most likely slope, environment (Jenkins 1992; Narbonne, Dalrymple, and Gehling 2001; Wood et al. 2001). The Trepassey Formation outcropping at Mistaken Point also contains deep-marine slope thin- to medium-bedded turbidites (Narbonne, Dalrymple, and Gehling 2001; Wood et al. 2001). Outcrops of the Fermeuse Formation have also been interpreted as deep marine in origin (Jenkins 1992).

TAPHONOMY

In the Ediacara Member (Figure 2.3), fossils of soft-bodied organisms are typically preserved in part-and-counterpart preservation as casts or molds on the soles of storm event beds with complimentary casts or molds formed on the top surfaces of underlying beds (Jenkins, Ford, and Gehling 1983; Gehling 1999) (Figure 2.6). Using trace fossil preservation terminology, fossils found on soles of sandstones as concave impressions are negative hyporeliefs, and casts in convex relief are positive hyporeliefs (Glaessner 1984; Seilacher 1989); preservation on the underlying sandstone beds thus occurs as epirelief counterpart casts and molds (Gehling 1999) (Figure 2.6).

Fossils that have been traditionally termed medusoids (Glaessner 1961, 1984) sometimes occur in an overlapping position or are pressed close together so they show apparent tears that may have occurred during physical battering (Wade 1972b; Jenkins, Ford, and Gehling 1983). Discoidal fossil forms are also preserved as mass kills, with some bedding planes covered with numerous individuals (Jenkins, Ford, and Gehling 1983). Frond-like fossils that have traditionally been identified possibly as sea pens are commonly torn free of their anchoring structures (Figure

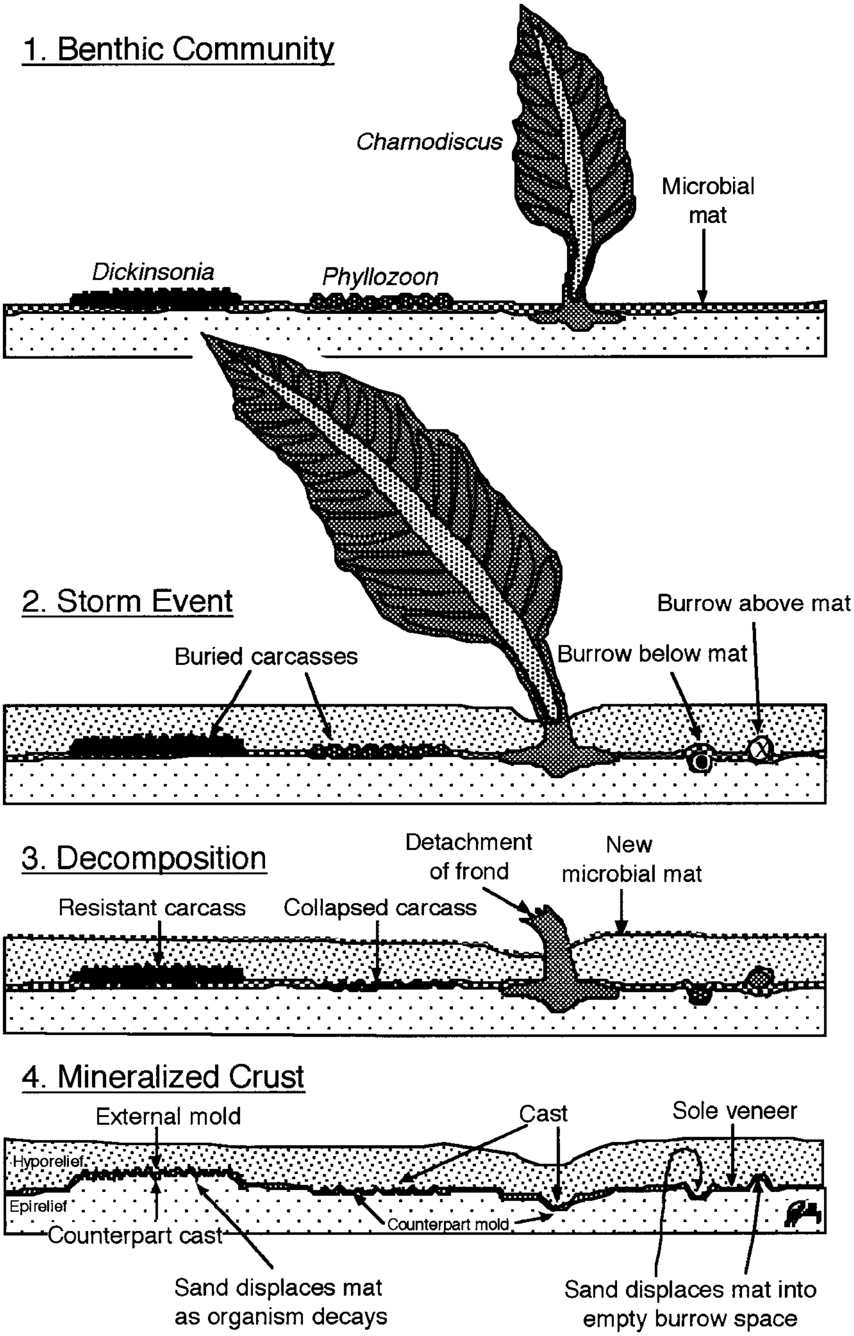

FIGURE 2.6 A schematic model for Ediacara taphonomy: (1) Benthic community of Ediacara biota on a microbial mat; prostrate *Dickinsonia* and *Phylozoon;* upright frond, *Charniodiscus.* (2) Storm event buries Ediacara organisms and mat; frond survives with buried holdfast; infaunal burrows made above mat and below mat. (3) Decomposition of organisms begins with rapid collapse of *Phylozoon* and slow decay of *Dickinsonia;* storm detaches frond, but new mat prevents erosion. Bacterial reduction of iron in the sole veneer. (4) Mineralized crust forms as a death mask in the sole veneer; after complete decay of organic material, the underlying sand forms epirelief counterpart casts and molds. (Modified from Gehling 1999)

2.6), which in a few instances can be seen to correspond with the discoidal forms, and some show evidence of decomposition (Jenkins, Ford, and Gehling 1983). None of the fossils in the Ediacara Member show any evidence of predation (Glaessner 1979).

The presence of actual trace fossils of infaunal bilaterians in the Ediacara Member (Glaessner 1969; Narbonne 1998) indicates that surface sediments and the overlying seawater were well oxygenated. Glaessner (1984) has postulated that the bodies of medusoids, although composed of 96 to 98 percent water, are sufficiently tough that they would not break apart with compaction, with continued decomposition and compaction eventually forming the molds and casts that are now found.

In the Briscal, Mistaken Point, and Trepassey Formations (Figure 2.5), fossils are preserved on the upper surfaces of beds that are overlain by graded volcanic ash layers, which range from a few millimeters to 0.5 m thick (Jenkins 1992; Narbonne 1998). These ash layers are interpreted to have originated from large nearby phreatomagmatic explosions that caused steam-buoyed ash to move in an apron across the sea (Jenkins 1992). Ash crystals would have settled quickly to the seafloor, and since the density of unskeletonized marine organisms is about that of seawater, these crystals would have settled faster than any Ediacara organism living in the water column (Anderson 1978; Jenkins 1992). Thus, it is generally agreed that this preserved Ediacara assemblage represents organisms that lived on the seafloor (Jenkins 1992). The preservation of these organisms involved their being pushed down into the underlying sand bed by the weight of the overlying ash (Jenkins 1992). As the organisms decayed, ash then filled the mold as decomposition proceeded (Jenkins 1992). In some examples, composite molds were produced; in other cases, the crystals of the tuff are coarse enough to obscure morphological details, so that morphological aspects of the fossils are commonly difficult to distinguish (Jenkins 1992), particularly where they have also suffered tectonic deformation.

Of utmost importance to understanding the Ediacara biota is that soft-bodied animals, such as jellyfishes, are not preserved in any younger rocks the same way as they are at sites with Ediacara fossils (Seilacher 1984). Seilacher (1984:161) has thus posed the question "Why did the Ediacaran mode of preservation become 'extinct'?" Possibly, Ediacara organisms had a flexible cuticle that was not digestible by contemporaneous microorganisms (Seilacher 1984), as is that of modern soft-bodied organisms. In a similar vein, Norris (1989) has concluded from experimental studies that Ediacara organisms had a stiff cuticle that is not as easily torn or folded as proposed modern analogues. Taphonomic studies by Crimes, Insole, and Williams (1995) on Late Cambrian examples of the Ediacara biota also led them to conclude that members of the Ediacara biota were not truly soft-bodied and that they had a rigid outer wall. Even though burrows made by bilaterians are found in the Ediacara Member (Glaessner 1969), they apparently did not scavenge the remains of buried Ediacara organisms, as would happen in modern well-oxygenated environments. Similarly, in a study analyzing three-dimensional preservation of the Ediacara fossil *Ernietta* from classic fossil localities in Namibia, Dzik (1999) concluded that the presence of the Ediacara biota in the fossil record is in large part because decomposers, which could consume collagen, had not yet evolved. From this analysis, Dzik (1999) further postulated that most Ediacara fossils do not represent the complete anatomy of the original organisms, but typically only the preservable internal hydraulic skeletons of these animals.

Although many studies on taphonomy of the Ediacara biota have concentrated on proposed degradational properties of Ediacara soft tissues, several recent studies have focused on the effects of microbial mats on the preservation of these fossils (Gehling 1986, 1999; Narbonne and Dalrymple 1992; Narbonne, Dalrymple, and MacNaughton 1997). Evidence is beginning to develop that, just as for carbonate substrates, Neoproterozoic siliciclastic seafloors were typically covered with microbial mats (Pflüger and Sarkar 1996; Hagadorn and Bottjer 1997, 1999; Bottjer, Hagadorn, and Dornbos 2000). Gehling (1999) has proposed that when event beds covered siliciclastic seafloors on which Ediacara organisms lived, the smothered microbial mats inhibited the vertical movement of pore fluids, hence promoting rapid cementation of a sole veneer in the overlying sand (Figure 2.6). In this way, the microbial mats may have acted as "death masks" for buried Ediacara organisms (Gehling 1999).

Thus, we still do not completely understand all the causes that led to preservation of Ediacara organisms and the specific contributions of the degradational behavior of Ediacara soft tissues versus characteristics of the environment, particularly the effects of microbial mats. However, since it now appears that some Ediacara fossils occur in the Cambrian, future studies will certainly focus on how this taphonomic window closed in the Proterozoic–Phanerozoic transition (Hagadorn and Bottjer 1997; Seilacher 1997; Jensen, Gehling, and Drosser 1998; Hagadorn, Fedo, and Waggoner 2000).

Paleobiology and Paleoecology

Fossils of soft-bodied organisms from the Ediacara Member have traditionally been referred to as still-extant phyla (Glaessner 1961, 1983; Wade 1972a, 1972b; Jenkins 1992) (Figure 2.7). Using this approach, members of the Cnidaria are most commonly identified, including forms that were solitary medusoids or polypoids (e.g., *Cyclomedusa, Ediacara*), frond-like fossils that are considered to probably be sea pens (e.g., *Charniodiscus*), as well as hydrozoans (e.g., *Ovatoscutum*), cubozoans (e.g.,

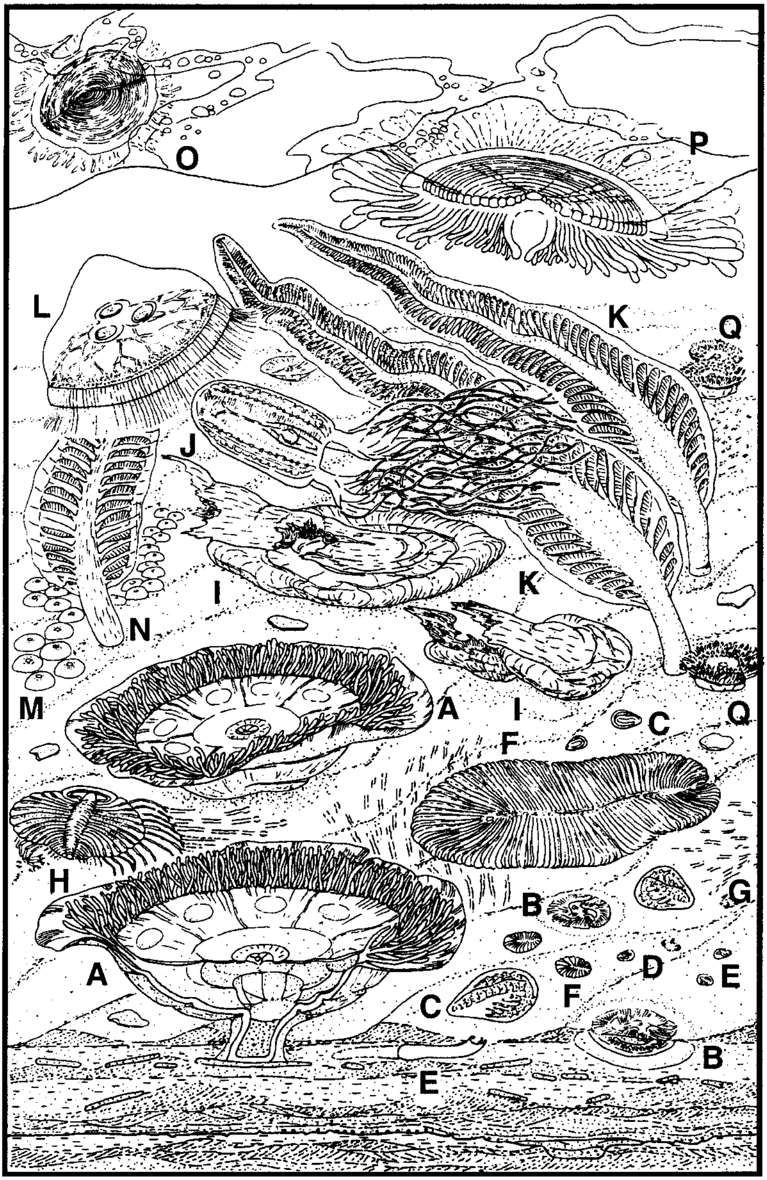

FIGURE 2.7 Reconstruction of subtidal biotas represented in the Ediacara assemblage of the Flinders Ranges, South Australia: (A) sectioned *Ediacaria flindersi* individual; (B) *Tribrachidium heraldicum;* (C) *Paravancorina minchami;* (D) *Praecambridium sigillium;* (E) burrowing organism with three sclerotized elements on anterior; (F) *Dickinsonia costata,* juveniles and mature examples; (G) scratch marks made by feeding epibenthos; (H) soft-bodied trilobite; (I) dead and torn specimens of *Cyclomedusa* partly exhumed from the substrate; (J) *Kimberella quadrata;* (K) *Charniodiscus longus;* (L) *Rugoconites enigmaticus;* (M) *Nemiana simplex;* (N) *Charniodiscus oppositus;* (O) *Ovatoscutum concentricum;* (P) *Eoporpita medusa;* and (Q) *Medusinites asteroides,* an anemone-like creature. Organisms are shown at varying scales to true natural size. (Modified from Jenkins 1992)

Kimberella), and scyphozoans (e.g., *Rugoconites*) (Figure 2.7). Other common fossils include those that are interpreted as polychaete worms (e.g., *Dickinsonia* [Figure 2.8], *Spriggina* [Figure 2.9]) and a representative (*Tribrachidium*) of a phylum, Tribrachidia, that is thought to occur only in the Ediacara biota and has been compared with the edrioasteroids (Glaessner 1984) (Figure 2.7).

Other than forms recognized from other sites, none of the members of the Ediacara fauna on the Avalon Peninsula in Newfoundland have been formally described (Jenkins 1992). However, initial assessment of the fauna indicates that it contains about 20 genera (Anderson 1978) with at least 30 species (Anderson and Conway Morris 1982). Jenkins (1992) has reconstructed some of these fossils as they may have existed in life (Figure 2.10). The following five main groups of fossils occur in decreasing order of approximate abundance (Jenkins 1992): (1) spindle-shaped forms (Figures 2.10–2.12) in the upper parts of the Mistaken Point Formation; (2) complexly branched forms (Figure 2.10), including the bush-like form, probably the Pectinate forms, and animals with numerous fronds joined by branching or zigzag connections, in the upper parts of the Mistaken Point Formation, the Trepassey Formation, and the lower Fermeuse Formation; (3) strongly frondose forms with stalks expanded basally or terminating in a disk (Figure 2.10), traditionally interpreted as sea pens, including *Charnia masoni* and about four

FIGURE 2.8 *Dickinsonia costata* from the Ediacara fauna of South Australia. Length of larger specimen is 13 cm. (Photo courtesy of B. Runnegar, University of California, Los Angeles)

FIGURE 2.9 *Spriggina flindersi* from the Ediacara fauna of South Australia. Length of specimen is 4 cm. (Photo courtesy of B. Runnegar, University of California, Los Angeles)

species that may be loosely grouped in *Charniodiscus* (Figures 2.11 and 2.12), from the upper part of the Mistaken Point Formation, the Trepassey Formation, and the lower Fermeuse Formation; (4) discoidal organisms (Figure 2.10), traditionally interpreted as medusoids, with either radial lobes or irregular lobes, found in the Briscal, Mistaken Point, and Trepassey Formations; and (5) discoidal organisms with strongly developed annulations, from the mid-Fermeuse Formation.

Seilacher (1984, 1989, 1992) revolutionized the study of Ediacara fossils by disputing the assignment of most of the Ediacara biota to still-extant phyla. He argued that the morphology of the Ediacara fossils interpreted as medusoids does not match that of Phanerozoic jellyfish fossils or of extant jellyfish. Bruton (1991) has studied preservation of modern jellyfish in the field and the laboratory, and believes his results show that casts and molds of modern jellyfish do not resemble the Ediacara fossils interpreted as medusoids. Similarly, Crimes, Insole, and Williams (1995) dispute the medusoid origin of certain Ediacara fossils. However, Norris (1989) studied preservation of modern jellyfish in the laboratory, compared his results with Ediacara fossils interpreted as medusoids, and concluded that one could not reject the contention that the fossils are in fact molds and casts of medusoids.

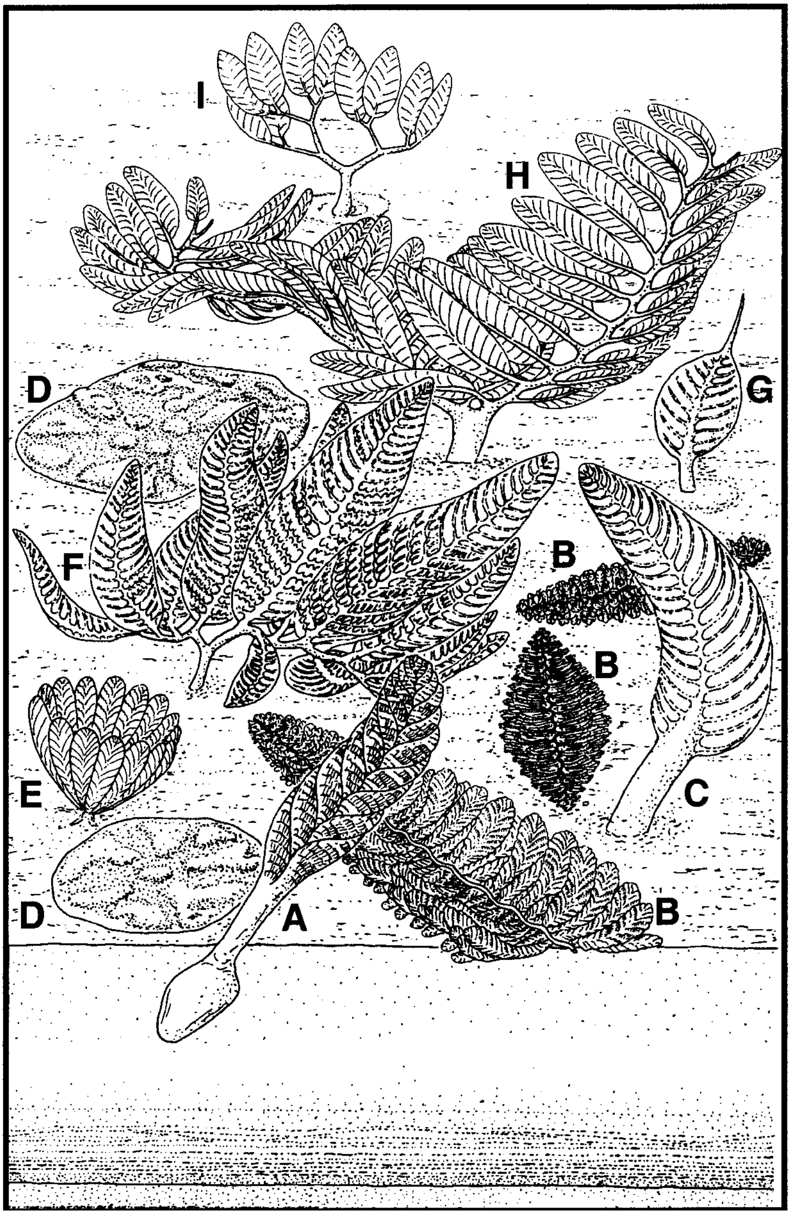

FIGURE 2.10 Reconstruction of Ediacara fauna from the upper part of the Mistaken Point Formation, Avalon Peninsula, Newfoundland: (A) *Charnia masoni;* (B) spindle-shaped fossils; (C) *Charniodiscus concentricus;* (D) lobate discoidal remains; (E) bush-like fossils; (F) branched frondose fossil; (G) *Charniodiscus* sp.; (H) pectinate organism; (I) dichotomously branched frondose organism. *Charnia* is approximately 18 cm long; all other organisms are shown at the same scale. (Modified from Jenkins 1992)

FIGURE 2.11 *Charniodiscus,* a frond-like fossil with a disk-shaped holdfast (*right*), with portion of a spindle-shaped fossil, from the Mistaken Point Formation, Avalon Peninsula, Newfoundland. *Charniodiscus* is 6.4 cm tall. (Photo courtesy of A. Seilacher, Tübingen University and Yale University)

Seilacher (1989) also questioned the assignment of the frondose forms to the pennatulaceans, or sea pens. He maintained that many of the supposed Vendian sea pens lack an axial stem (possessed by modern sea pens) and that all the fronds of the Ediacara sea pens are leaf-like structures without branch separation. Modern sea pens have branch separation so that currents can pass through, thus allowing polyps on the branches to feed (Seilacher 1989). Similarly, Seilacher (1989) contested the assignment of *Dickinsonia* to the polychaete worms.

As an alternative model for understanding the biology of many Ediacara soft-bodied organisms, Seilacher (1989, 1992) proposed that they shared a serially or fractally quilted pneu structure, similar to that of an air mattress, that allowed them to build a relatively rigid, broad flat organism. Because no real organs have been identified in Ediacara fossils, Seilacher postulated that these organisms may have operated their metabolic processes (nutrient uptake, respiration, excretion) through the body surface, in which case maximizing surface area through such a pneu structure would be advantageous (Seilacher 1989). Analysis of several specimens of *Dickinsonia* has led Seilacher (1989) to conclude that the quiltings were attached together by rigid internal struts rather than a continuous sheet, such as is found in an air mattress.

FIGURE 2.12 Four *Charniodiscus* and at least 12 spindle-shaped fossils from the Mistaken Point Formation, Avalon Peninsula, Newfoundland. Slab surface is 70 cm across. (Photo courtesy of A. Seilacher, Tübingen University and Yale University)

Animals that employ this quilted structure were termed the Vendobionta by Seilacher (1992), and they represent a phylogenetically distinct animal group of kingdom or phylum rank (Seilacher 1992; Buss and Seilacher 1994). In this interpretation, Seilacher (1989, 1992) acknowledged that other metazoans coexisted with the Vendobionta and that they have left a fossil record in the form of trace fossils. Seilacher's (1984) earlier work on the Ediacara biota suggested that their large surface areas would be advantageous for organisms that were photosymbiotic. However, the presence of Ediacara fossils in strata deposited below the photic zone (e.g., Mackenzie Mountains of northwestern Canada) indicates that at least some Ediacara organisms did not need sunlight to live, and hence were probably not photosymbiotic (Seilacher 1992).

McMenamin (1986) and McMenamin and McMenamin (1990) proposed that members of the Ediacara biota may have been well adapted for chemosymbiosis, using as an analogy the chemosymbiotic organisms that live at modern hydrothermal vents and cold seeps. McMenamin and McMenamin (1990) acknowledge that there is no evidence for hydrothermal activity in deeper-water strata in which the Ediacara biota is found, nor is there evidence for fossil cold seeps. McMenamin and McMenamin (1990), however, do suggest that these organisms may have been trapping a diffuse methane or hydrogen sulfide flow from the seafloor to fuel their chemosymbiotic activity. Seilacher (1989) also proposed that members of the Ediacara biota may have been chemosymbiotic and that the microbial mats covering Proterozoic seafloors produced a sharp boundary between oxygenated bottom-water and reducing pore waters, allowing broad, flat Ediacara organisms to adsorb hydrogen sulfide or methane through their bottom surface and oxygen through the exposed upper surface. In a study of the Mackenzie Mountains Ediacara fossil locality from northwestern Canada, Narbonne and Dalrymple (1992) interpreted the depositional environment as deep-sea, and found that the Ediacara fossils were associated with pyritic intervals that also show evidence of microbial mats. Narbonne and Dalrymple (1992) suggested that the microbial mats aided preservation of these fossils (Narbonne, Dalrymple, and MacNaughton 1997), much as has been proposed for shallow-water Ediacara fossils by Gehling (1986, 1999). Narbonne and Dalrymple (1992) also postulated that these particular Ediacaran organisms lived under exaerobic conditions (Savrda and Bottjer 1987), which potentially supply additional support for the chemosymbiosis hypothesis.

Some members of the Ediacara biota attained relatively large sizes—up to 1 m long for some specimens of *Dickinsonia*. Although these large organisms would represent a ready food source for predators, no evidence of predation on them or any other Ediacara organisms has been found. Thus, McMenamin (1986) has termed this "The Garden of Ediacara" because it was a world with no apparent predators of Ediacara organisms.

Until recently, it was believed that the Ediacara biota became extinct before the beginning of the Cambrian. This disappearance of the Ediacara biota before the Cambrian was thus interpreted as a mass extinction due to the evolution of the first predators, which presumably were non-Ediacara metazoans (McMenamin 1986; Seilacher 1989; McMenamin and McMenamin 1990). The discovery of members of the Ediacara biota through the late Proterozoic and into the Cambrian (Conway Morris 1993; Crimes, Insole, and Williams 1995; Grotzinger et al. 1995; Jensen, Gehling, and Drosser 1998; Hagadorn, Fedo, and Waggoner 2000), however, indicates that the history of the Ediacara biota cannot be easily separated from that of other Phanerozoic organisms.

A diverse and stimulating array of data and ideas continues to be generated on the nature of these fossils. For example, based on a comparative taphonomic analysis, Retallack (1994) proposed that the Ediacara biota may actually represent fossil lichens, an idea that has generated much discussion (Retallack 1995; Waggoner 1995). Taking a different view, Steiner and Reitner (2001) have postulated that some Ediacara organisms were procaryotic colonies or symbiotic organisms involving procaryotes. In contrast, however, many students of this biota continue to support conclusions that although a number of Ediacara fossils certainly appear to be strange, they are genuinely ancestors of metazoan groups we know today. Thus, Valentine (1992) has interpreted *Dickinsonia* as a benthic polypoid that is very likely of cnidarian affinity, and Fedonkin and Waggoner (1996) have postulated that *Kimberella,* originally described as a cubozoan medusa, actually is the fossil of a benthic mollusc-like organism. Similarly, Buss and Seilacher (1994) have suggested that the Vendobionta are a monophyletic sister group to the Eumetazoa and were cnidarian-like organisms that lacked cnidae. Dzik's (1999) hypothesis that the complete anatomy of Ediacara organisms may not be preserved as fossils, as well as the interpretation by Grazhdankin and Seilacher (2002) that some members of the Ediacara biota were infaunal, may also have important implications for ultimately understanding the biological affinities of this fauna.

As we learn more about the phylogenetic affinities and functional morphology of the Ediacara fossils, we will be able to reconstruct the paleoecology of these organisms in more detail. A beginning has already been made by Seilacher (1997; Seilacher and Pflüger 1994), who has postulated that benthic Ediacara organisms were specifically adapted for a microbial mat–covered seafloor. Thus, various Ediacara organisms (such as the mollusc *Kimberella*) fed on the mat surface and hence were *mat scratchers,* while others (such as *Tribrachidium*) were firmly attached to the mat surface and were *mat encrusters.* Narbonne (1998) has proposed that the Ediacara fauna represents the initiation of complex ecological tiering, with three feeding levels: an elevated level in the water column occupied by fronds; a seafloor level with a variety of organisms, including mat encrusters and scratchers; and a subsurface level represented by trace fossils made by bilaterians (Ausich and Bottjer 2001).

CONCLUSIONS

The Ediacara biota represents more than just another example of exceptional fossil preservation. Younger marine Lagerstätten are usually in fine-grained sediments and are recognized because they contain (1) soft-bodied members of a fauna that also contain taxa with mineralized skeletons, (2) preservation of soft tissues of organisms that also have mineralized skeletons, or (3) articulated skeletons of organisms that are usually preserved disarticulated. Other than evidence on sponges (Brasier, Green, and Shields 1997; Li, Chen, and Hua 1998) and bilaterian trace fossils, as well as initial results on cnidarians (Chen et al. 2000; Xiao, Yuan, and Knoll 2000) and bilaterian embryos and larvae (Chen et al. 2000), the Ediacara biota represents most of the currently known evidence of metazoan life that existed during the Neoproterozoic. Thus, it does not provide supplemental information, but much of the information on possible metazoan life at this time. Because we are only just beginning to understand how to investigate Lagerstätten, as compared with the typical Phanerozoic assemblage with mineralized skeletons, study of the meaning of the Ediacara biota is doubly difficult.

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