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Assemblage palaeoecology of the Ediacara biota: The unabridged edition?

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Abstract

Fossils of the Ediacara biota offer our earliest insight into diverse macroscopic life on this planet. In particular, given the diversity and range of exquisite soft-bodied preservation, the potential for unraveling aspects of the paleobiology and paleoecology is great. Clearly, however, there can be a taphonomic overprint that dictates how complete the assemblage is. New diversity data (including richness and evenness) from South Australia is compared to previously published data from Newfoundland and the White Sea and is within the range of values for both modern and Phanerozoic assemblages. However, missing from our current understanding of Ediacaran ecosystems is a full description and interpretation of the many problematica structures and organic surfaces.

Keywords: Ediacara biota; Neoproterozoic; Flinders; Taphonomy; Paleoecology

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1. Introduction

Ediacaran strata contain the earliest diverse macroscopic fossils, the so-called Ediacara biota, known from numerous localities globally (Narbonne, 1998, 2005). Traditionally, the majority of these fossils, generally preserved as casts and molds in siliciclastic sediments, were placed in modern animal phyla. Radially symmetrical and sea pen like forms have generally been assigned to the Cnidaria and segmented more or less bilaterally symmetrical forms identified as having affinities to annelids and arthropods (e.g. Glaessner, 1984; Gehling, 1991). Problems in finding unequivocal morphological characters linking them to modern phyla as well as their unusual style of preservation recently prompted suggestions of alternative taxonomic affinities ranging from an extinct kingdom of “Vendobionts” (Seilacher, 1992), mesozoans (McMenamin, 1998), prokaryotic colonies (Steiner and Reitner, 2001) protists (Zhuravlev, 1993), lichens (Retallack, 1994), and fungi (Peterson et al., 2003). Lately, however, a consensus has emerged that at least some Ediacara-type fossils are indeed cnidarian and bilaterian metazoans but that their closer affinities remain problematic. In addition, there are forms that are likely non-metazoans (e.g., Runnegar, 1995; Waggoner, 1998; Valentine, 2001; Peterson et al., 2003).

Previous work on the Ediacara biota has focused on: 1) Systematic affinities and palaeobiological reconstructions of individual taxa. (e.g., Glaessner and Wade, 1966; Wade, 1972; Jenkins, 1985, 1992; Gehling, 1987,

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1988; Ivantsov and Grazhdankin, 1997; Gehling et al., 2000; Ivantsov, 2001; Fedonkin and Waggoner, 1997; Dzik and Ivantsov, 2002); 2) The taphonomy of Ediacara-type organisms including the role of microbial mats in their preservation (Wade, 1968; Seilacher, 1992; Gehling, 1999) and 3) Biogeography and stratigraphic range, including the possibility of an end-Ediacaran mass extinction (e.g., Brasier, 1995; Jensen et al., 1998; Waggoner, 1999; Hagadorn et al., 2000; Martin et al., 2000; Narbonne et al., 2001; Gehling and Narbonne, 2002). Narbonne (2005) reviews many of these aspects of the Ediacaran biota.

All of these venues of research have led to a much more detailed picture of Ediacaran macroscopic fossils. However, one aspect of the Ediacara biota that remains less well understood and yet is critical for our understanding of the palaeobiological and palaeoecological relevance of Ediacara fossils is the ecological structure and synecology of Ediacara assemblages. The Ediacara-type fossils and preservation is considered one of the major fossil lagerstätten alongside a number of Phanerozoic examples such as the Burgess Shale and Solnhofen (e.g. Bottjer et al., 2002; Selden and Nudds, 2004). The Ediacara-type assemblages are in fact unique in having bedding-planes that preserve benthic non-mineralized organisms that appear not to have been transported. Recently, the synecology of Ediacaran organisms has received attention with the recognition that these well exposed bedding planes—in particular from Newfoundland, the White Sea of Russia as well as new material from South Australia—provide in situ community scale data unsurpassed in the fossil record. There are, however, formidable problems in the study of Ediacaran synecology. An obvious initial obstacle is that the autecology of most of these organisms is poorly understood though it has been discussed at great length in the literature because of the relevance to taxonomic affinities. That is, for example, *Dickinsonia* has been variously interpreted as an annelid, lichen, fungi or even as belonging to an extinct kingdom. Each one of these interpretations requires a very different autecology. Another possible source of uncertainty, and one likely related to autecology, is that these organisms may have been adapt to benthic environments that do not have a direct comparison for most of the Phanerozoic. An important factor in the study of Ediacaran paleoecology is that microbial mats were developed to a much greater extent in the Proterozoic than for most of the Phanerozoic. In the absence of significant disruption by burrowing animals their development was limited mainly only by physical reworking. Particularly in subtidal environments within the photic zone microbial mats appear to have been widely developed. These mats sealed the surface sediment rendering it less prone to erosion. The presence of these microbial mats as well as the low levels of bioturbation would have resulted in a sharp gradient from oxic surface water to anoxic surface sediment (Seilacher, 1999; Droser et al., 2002).

The majority of the macroscopic organisms known from the Ediacaran appear to have been living in close association to these mats. Due to the sharp redox gradients across the microbial mats it has been suggested that a number of the organisms may have had photo- or chemoautotrophic symbionts (e.g. Dzik, 2003), in particular the various radial forms. Indeed, it has been suggested that microbial mats may have structured early metazoan benthic life (Gehling, 1999; Seilacher, 1999; Bottjer et al., 2000). Seilacher (1999) recognized four principal types of mat-related life styles: mat encrusters, attached to the top of the mat-bound sediment; mat scratchers, grazing on the mats; mat stickers, partly emerged in the mats and growing upwards as the mat-level changed; and undermat miners, tunneling beneath the mat. Several of these strategies also seem to have persisted into the earliest Cambrian (Seilacher, 1999; Bottjer et al., 2000; Dornbos et al., 2005). Microbial mats apparently were not restricted to the photic zone but have also been recognized in deep water Ediacaran assemblages (e.g. Clapham et al., 2004).

Thus, while Ediacaran assemblages potentially provide the best opportunity in the fossil record to examine in situ paleoecology (for example, Burgess Shale fossils were transported) the irony is that we are working with fossils that 1) represent organisms that lived in a very different benthic setting than those of the past 540 million years and, that 2) we do not understand in terms of their autecology or affinities. However, given the otherwise superb nature of the fossils, the question is can we constrain the synecology of these assemblages? In this context, in this paper, we review the nature of the Ediacaran record, review previous work on Ediacaran assemblages from the White Sea and Newfoundland and compare these data with new data from South Australia. These three primary areas make for a useful comparison of Ediacaran paleoecology because they represent a variety of environments and cover a range of taxonomic diversities. Additional data from Namibia is also discussed. Furthermore, fossils at Ediacaran localities globally cluster into three main biofacies or assemblages: 1) the Avalon Assemblage (including Newfoundland fossils), 2) the White Sea Assemblage (also including South Australia fossils) and 3) the Nama Assemblage (Gehling et al., 2001; Waggoner, 2003) and thus we can compare within a cluster and between two clusters.

2. The stratigraphic range of Ediacara-type fossils

Globally three Ediacara associations have been recognized and interpreted as evolutionary stages (Gehling and Narbonne, 2002), paleogeographic zones (Waggoner, 1999, 2003) and biofacies without significant time separation (Grazhdankin, 2003). The Avalon assemblage, bracketed by dated ash beds as 575 Ma (Bowring et al., 2003) to less than 565 Ma (Benus, 1988), is the oldest. The White Sea assemblage is the next oldest, at 558–550 Ma (Martin et al., 2000), and the Nama assemblage dated between 549 and 543 Ma (Grotzinger et al., 1995) extends to the base of the Cambrian. The Ediacara fossils from South Australia cluster within the White Sea assemblage (Waggoner, 2003).

Biostratigraphic subdivision of the Ediacaran, based on Ediacara assemblage zones, is contingent on evidence that the three Ediacara fossil assemblages are sequential rather than biogeographic or environmental associations. All of the known examples of the Avalon assemblage come from successions in deeper water settings than those of the White Sea or Namibia assemblage. The lack of trace fossils and bilaterian body fossils is notable in the Avalon assemblage from all three of the earliest documented successions, namely, the Conception Group of SE Newfoundland (Narbonne and Gehling, 2003), the Charnwood Group in England (Boynton and Ford, 1995), and in the Sheepbed Formation of NW Canada (Narbonne and Aitken, 1990). This is more likely to be a function of the evolutionary stage, rather than environmental, because key frondose taxa, like *Charnia* and *Charniodiscus*, are known from the apparently shallower water White Sea assemblage. Grazhdankin (2004) claims that these three assemblages reflect different sedimentary facies in the White Sea succession and do not represent a biostratigraphic succession. However, since key taxa from the Avalon and Nama assemblages are absent from the White Sea assemblage, it is premature to argue that these assemblages are included in the White Sea succession. The analysis of the distribution of Waggoner (2003) of the Ediacara biota in time and space showed that there was considerable disparity in the distribution of Ediacara taxa in time and space. He concluded that fronds and discs had the widest geographic distribution and longest time ranges, and the bilaterian taxa were less cosmopolitan due to their later arrival on the scene. The overlap between assemblages, which includes Ediacara index fossils such as *Charnia*, *Pteridinium* and *Palaeopascichnus*, demonstrates the wide stratigraphic, environmental and paleogeographic ranges and basic unity of the Ediacara biota.

3. Nature of the Ediacara fossil record

Paleoecological interpretations of Ediacara fossils are directly tied to the preservational history. For example, are we selectively preserving those organisms living under mats or above mats? Thus, before any paleoecological questions can be asked it is important to ask: how strong is the taphonomic overprint on the preserved paleoecology?

The preservation of external molds of soft, unmineralized organisms has always been one of the major stumbling blocks for those questioning the heterogeneity of Ediacara organisms. Our amazement at the preservation of detailed impressions of soft-bodies in coarse siliciclastics can now be damped by better understanding of the peculiar taphonomic mechanisms that opened this unique fossil window (Gehling, 1999). In South Australia and Namibia, Ediacara fossil impressions preserved in sandstone show little primary evidence of the mineralized death-masks thought to have been responsible for conserving external molds of soft organisms. However, there is secondary mineral evidence. The fossil-bearing sole surfaces are characteristically coated in iron oxides. In many cases, beds composed of clean, white quartz arsenite have red soles. The sole-veneer of sand grains is coated with iron oxides. Likewise fossiliferous partings in otherwise massive beds of sandstone are coated in iron oxides.

In Northwestern Canada, Ediacara fossils from the Windermere Supergroup are most often associated with carbonaceous partings suggesting organic rich substrates (Narbonne and Hofmann, 1987). However, the limited presence of iron oxides on these surfaces may explain the very spare record of fossils preserved as external molds in the Sheepbed and Blueflower formations.

The key evidence that mineral death masks were an important agent in Ediacaran fossilization is found in the White Sea region of NW Russia (Dzik, 2003). Fedonkin and Waggoner (1997) reported that *Kimberella* was preserved on surfaces coated with framboidal pyrite. Grazhdankin (2003) has described freshly excavated bedding surfaces coated with pyritized filaments, from the Erga Formation of the White Sea region, in Russia. Fedonkin (personal communication) noted that the pyrite oxidizes to limonite soon after exposure to the atmosphere. Dzik (2003) also identified “intact” microbial mats in the Mezen Formation at the Zimnie Gory locality of the White Sea.

A variety of other characteristics of fossiliferous beds points to early cementation of selective laminae. Microfaults in fossiliferous sole surfaces are not propagated through the entire bed, suggesting very early post-depositional dislocation of strata. Fossils are known from the soles of large load balls where pull-apart cracks cut fossil molds but no not penetrate into the overlying laminae. Such post-depositional features point to very early and selective cementation for the sole-veneer of smothering sand (Gehling, 1999, 2000).

In SE Newfoundland, fossiliferous surfaces in the Conception Group are the product of smothering by both crystal tuffs and finer ash falls. The ash layers produced a “Pompeii effect” by blanketing the benthic communities (Narbonne et al., 2001). Organisms already lying on the substrate were cast with precision, while those floored by the ash falls were less well molded. While in other Ediacara assemblages, fronds are commonly preserved in positive hyporelief (but see Dzik, 2002), in the Conception Group they are preserved in positive epirelief as casts of ash molds. This suggests that the “death masks” formed before collapse of the organism due to rapidly cementing volcanic ash sediment. However, the presence of biomats is implied by the frequent preservation of reticulate textures on these surfaces. Like Ediacara fossil beds elsewhere, most of the fossiliferous surfaces in the Conception Group have iron-oxide stained surfaces. This feature is used in searching for fossil bearing surfaces in this extremely thick succession of deep-water volcaniclastic sediment.

In South Australia, our recent efforts to study fossils in stratigraphic and sedimentary context, and to assess the frequency of fossil beds in a particular sedimentary facies, have revealed surprising new information. Almost all the described taxa preserved as external molds are now known from part and counterpart associations. The previously assumed presence of clay- or slit-separated fossiliferous surfaces has been shown to be rare or absent. Moreover, there is no evidence of a gap between part and counterpart fossil impressions. Where one might expect sand covering a body to collapse into the body space as the organism decays, the contrary is true. The sand laminae from the substrate defied gravity and cast external molds from below. This single fact supports the notion of a mineralized death mask more than any other.

The process of bacterially precipitation of pyrite above molded bodies and the organic-rich or mat coated substrate (Gehling, 1999) can be expressed as a simple set of chemical reactions that depended on the presence of iron in the sediment and sulfate in the seawater trapped within the sediment (Fig. 1). The biomats were the source of bacterial decay following the sedimentary event that smothered, but did not erode, the substrate. If the interval between sedimentary events was sufficiently long, a new biomat was established over the new substrate, thus effectively sealing off the buried surface from oxidizing seawater. The bed thickness, grainsize and permeability of the preserving sand were some of

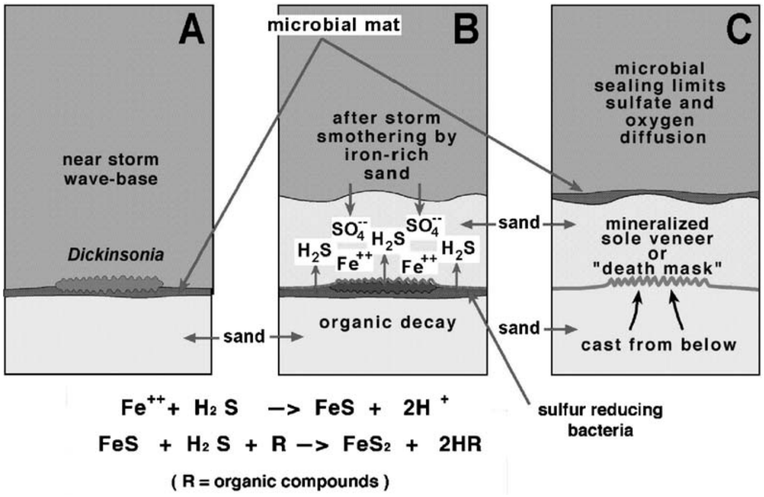

Fig. 1. (A) Mat covered Edicaran substrate with *Dickinsonia*. (B) Smothering by sand and bacterial decay and reduction of sediment iron in the presence of seawater sulfate. (C) Pyrite cemented sole veneer acts as a death mask preserving substrate relief and an external mold of *Dickinsonia*. Casting of the *Dickinsonia* mold is made by the uncemented sand below the original mat. The sand bed is sealed with a new microbial mat which limits further sulfate and oxygen diffusion from the water column.

the parameters involved in determining the rate of formation of a mineral death-mask over discrete bodies and the organic rich surfaces on which they lay. Sole surfaces where the textural relief was strongest and the diversity of organic debris was greatest are considered to be those exposed longest before another sedimentary event. High relief molds of particular taxa tended to occur in settings where sand was fine and the interval between depositional events was most protracted. These fossil beds most often came from the deeper water facies where bedding of the fossil bearing sandstones was generally thin, but intercalated with odd massive beds, representing stronger storm events.

While there are still many anomalies with this taphonomic paradigm, there is now a better understanding that Ediacara bodies were not made of extraordinary materials, but rather that they were a product of a world where, once buried, organisms were left undisturbed by all except bacteria, or later exhumation by mechanical erosion. Otherwise, there is no reason why Ediacaran assemblages cannot be viewed in much the same way as Phanerozoic communities; they probably involved metazoan animals, plants and even megascopic bacterial colonies.

Furthermore, it is our contention that the majority of Ediacara bedding-plane assemblages represent samples of benthic communities preserved in situ, though it is important to note that the same species may be preserved in several modes (Dzik, 2003). These fossil assemblages represent snap-shots, but how complete they are?

4. The other Ediacaran macroscopic record: trace fossils and organic structures

While discrete body fossils, such as *Dickinsonia* and *Charniodiscus*, provide the classic image of Ediacaran fossils, a significant proportion of the Ediacaran record is that of trace fossils and problematica in the form of organic surfaces and structures that may or may not be trace fossils. The abundance of these structures, commonly covering bedding planes and/or discrete structures comprising over half of an assemblage indicates the ecological significance of these structures.

Ediacaran sediments show evidence for activity within the sediment in the form of simple trace fossils. These are important in the study of the Ediacaran assemblages as they remain the only uncontested evidence of bilaterians (e.g. Budd and Jensen, 2000). Ediacaran trace fossils have been described by among others Glaessner (1969), Fedonkin (1977, 1980), Narbonne and Hofmann (1987), Narbonne and Aitken (1990). Indeed, a respectable number of ichnotaxa have been described from the Ediacaran (e.g. Crimes, 1992). However, it is becoming increasingly clear that the diversity of Ediacaran trace fossils has been overinflated.

The inflation in the number of ichnotaxa can in part be explained by structures that resemble trace fossils and that may include microbial mat structures as well as algal lawns or even degraded residues of body fossils. Importantly, in recent years, workers have recognized that both algal and metazoan body fossils are preserved as casts and molds in Ediacaran siliciclastics. Previously workers were not expecting to find algal, microbial and certain body fossils such as *Cloudina*, in siliciclastics and thus, most structures thought to be biogenic in origin were interpreted as trace fossils. Additionally, part of the problem in the study of Ediacaran trace fossils has been the identification based on fragmentary material. For example, a gently tapering narrow tubular fossil may easily be identified as a trace fossil if only viewed on a small fragment of rock. In fact, Ediacaran siliciclastic sediments yield a rich variety of largely undescribed elongate tubular organisms. Many of these have been classified as trace fossils but their mode of preservation and detailed morphology show that they are more likely body fossils (e.g. Runnegar, 1994; Jensen, 2003). A wide range of isolated or grouped round or elongate objects have been described as *Palaeopascichnus*, *Yelovichnus*, *Intrites* and “*Neonereites*”. While the origin of these structures is still debated most authors no longer consider them to have a trace fossil origin (Seilacher et al., 2003; Haines, 2000; Jensen, 2003).

The most characteristic undoubted traces are simple essentially horizontal forms made close to the sediment water interface. These traces are commonly found as corresponding grooves and ridges on sandstone surfaces. The mode of preservation suggested that their stratinomic position was controlled by the utilization of decaying microbial mats (Seilacher, 1999; Gehling, 1999). The manner in which sediment is displaced suggests that sediment was pressed aside rather than manipulated by any organs specialized in manipulating sediment. There has, for example, been recent interest in priapulids as producers of early trace fossils, particularly in the earliest Cambrian (e.g. Valentine, 1995; Dzik, 2005). However, the producers of Ediacaran trace fossils will remain unknown unless direct associations to the producing organisms are found.

The concentration of microbial mats and organic debris in varying states of decay would also seem to explain an unusually diverse array of textures associated with Ediacara-type fossils. Ediacaran bedding planes are, in fact, rich in problematic structures and surfaces that can be difficult to characterize and thus, have not entered the literature in a thorough or systematic way. Nonetheless, the ubiquity of these structures shows that they are important to a fuller understanding of Ediacaran communities. The interpretation of the precise origin of these structures is problematic. Characteristic textures occurring on Ediacaran fossiliferous surfaces in South Australia (Gehling, 1999, 2000), NW Canada (Narbonne, 1998) and the White Sea (Grazhdankin and Ivantsov, 1996) are regarded as evidence of microbial and algal mats. There has recently been increased interest in microbially induced sedimentary structures (e.g. Noffke et al., 2001). Here we use the term "organic surfaces" for sedimentary surfaces that have textures showing the interaction of sediment with microbial mats, but which generally lack distinctly preserved fossils.

These may occur in patches but may also cover complete bedding surfaces and generally are internally consistent, such as elephant skin or wrinkle marks (e.g. Hagadorn and Bottjer, 1997). In the Flinders' material, there is a particularly high diversity and abundance of organic surfaces (Fig. 2). Notably, in some cases, recognition of well-defined, regular elements in these "algal carpets" suggests macrophytic algae as an alternative to bacterial and even sedimentary origins. Regardless, these problematic structures, which are generally excluded from study, clearly represent a significant part of the ecosystem.

5. Ediacaran paleoecology

5.1. Previous paleoecological work

Previous studies of the syn-paleoecology of the Ediacara biota (e.g. Grazhdankin and Ivantsov, 1996; Grazhdankin and Seilacher, 2002; Gehling et al., 2000; Clapham et al., 2003) have made significant contributions to further our understanding of Ediacaran ecosystems. Here we compare the paleoecology of three classic Ediacara field areas where the community ecology has been examined. In addition, we discuss some material from Namibia. These three areas make for a useful comparison of Ediacaran paleoecology because they represent different depositional environments and cover a range of taxonomic diversities. The White Sea material has previously been discussed by Grazhdankin (2003, 2004) and Fedonkin (2003). The Avalon material has been specifically studied for assemblage paleoecology by Clapham and Narbonne (2002) and Clapham et al. (2003), The South Australian material is newly presented in this paper.

Before discussing the three main areas we will briefly examine paleoecological data from the Nama assemblage. Overall, data is very scarce due to limited bedding plane exposure and scarcity of fossils, especially in the western USA. At present Namibia provides the only information. A 30–50 cm thick bed of the Dabis Formation Kliphoek Member), at Aar Farm in Southern Namibia, with large numbers of three-dimensionally preserved specimens of the tri-vaned form, *Pteridinium,* has been studied in some detail by Grazhdankin and Seilacher (2002) at Aar Farm in Southern Namibia. Specimens are strongly distorted at some levels in this bed, while at other levels they are oriented in the same direction. Grazhdankin and Seilacher (2002) interpreted these as organisms preserved in situ, where they had been living and growing in the sediment, on the basis of one example of two apparently inter-grown specimens. Though Ivantsov (2001) interprets a more complex organization from three-dimensionally preserved specimens of *Pteridinium* and *Vantagyrus* from the Syuzma River White Sea locality. However, our studies of this bed suggested transport of specimens in sand flows that distorted many specimens and aligned others. In the Spitskop Member of the Urusis Formation. The current-oriented specimens at the top of the bed were preserved with all three vanes vertical and apparently intersecting the upper surface of the bed. Thin-sections of the tubular walls at the commissure of the three vanes show sand partly filling the tubes. Most often the tubes were collapsed near the margin. The thin sections and composite molds of collapsed tubes clearly demonstrated the hexagonal shape of the tubes and the fact that they were open at the outer margins of the vanes.

5.2. The White Sea

The Neoproterozoic siliciclastic succession in the White Sea demonstrates a range of siliciclastic lithofacies occurring over a 550 m thick succession (Grazhdankin, 2004). Extensive work has been done on the White Sea Ediacaran Biotas (e.g. Ivantsov and Grazhdankin, 1997; Ivantsov, 2001; Dzik, 2002, 2003; Fedonkin, 2003). Grazhdankin (2004) characterized several assemblages of Ediacara fossils in sections in northern Russia based on excavations of beds a few to several square metres. Most exposures are actively eroding cliffs or riverbanks (Grazhdankin, 2003). The sediment lacks induration and thus outcrops cannot be

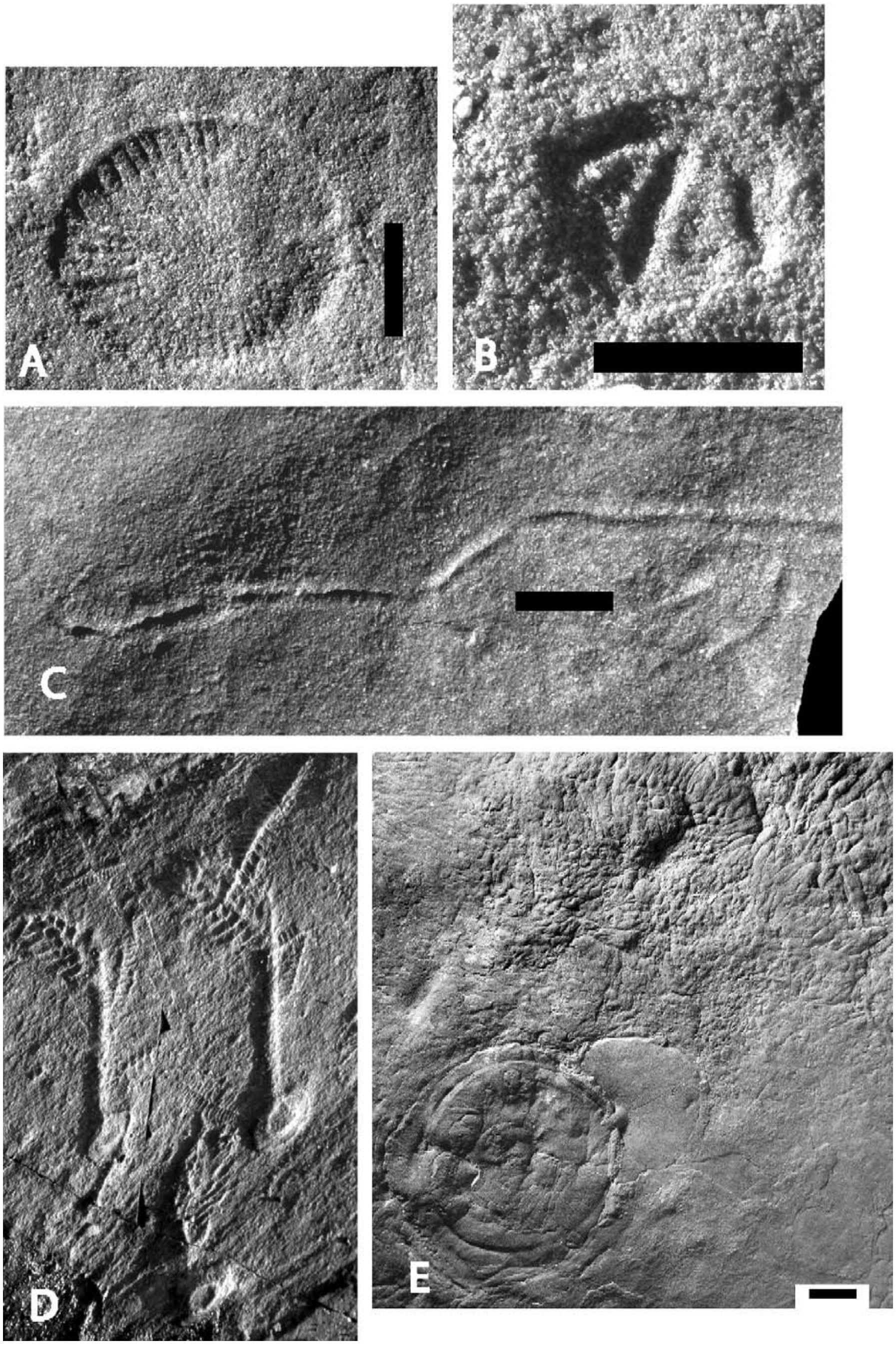

Fig. 2. (A) *Dickinsonia* preserved on the base of bed 3 at Mt. Michael, South Australia. (B) *Parvancornia* from the base of Bed 3 from Mt. Michael, South Australia. (C) Form B trace fossil from the top of Bed 3, Mt. Michael. (D) *Aspidella* disk preserved on the base of a bed with associated organic surface. Bed 2 Mt. Michael, South Australia. Disk would have originally been underneath the organic surface. *Charniodiscus procerus* and *Charniodiscus spinosa* on the top of a bed at Mistaken Point, Newfoundland. Scale bar in all photographs is 1 cm.

conserved between seasons. However, excavations of several square meters of fossiliferous surface have been achieved (e.g., Ivantsov and Malakovskaya, 2002).

Five lithofacies are present, each apparently with a distinct fossil assemblage: 1) a laminated shale lithofacies interpreted as representing deposition as a low-energy lower shoreface setting with the monospecific *Inaria* assemblage, 2) Alternating shale and siltstone representing deposition on storm-influenced middle shoreface with a *Charnia* assemblage, 3) interstratified sandstone and shale interpreted as deposited as upper-shoreface prodelta deposits with a *Dickinsonia-Kimberella* assemblage, 4) interstratified sandstone where individual beds are regarded as the product of single flood events in a fluviomarine setting with a *Onegia-Rangea* assemblage, and 5) amalgamated sandstone representing the infilling of broad and shallow distributary channels with only the enigmatic structure, "Arumberia".

5.3. Newfoundland

The Avalon succession on the Avalon Peninsula preserves over 100 fossiliferous bedding planes through a thickness of 2.5 km, spanning the Conception Group and the lower part of the St. Johns Group. The original surfaces were smothered with volcanic ash that preserves in situ communities. The strata are characterized by deep-water turbidities and have no features that are suggestive of wave influence or emergence.

Paleoecological studies are governed by chance exposure of surfaces exposed as a consequence of the weathering of prominent ash beds that could be accessed, along the coast of SE Newfoundland. There was no possibility to perform excavations and examine successive beds. Furthermore, the detail on these surfaces is somewhat compromised by strong cleavage, patchy adhering of ash and mechanical weathering of these volcaniclastic sediments. It is not possible to study successive bed assemblages; rather the community samples are separated by metres to hundreds of metres of strata.

Wood et al. (2003) have concluded that the Mistaken Point assemblages lived on a deep-water slope below wave base and the Photic zone. The oldest complex Ediacara fossils are found nearer the base of the succession, in the Drook Formation, above the Gaskiers Formation tillites (Narbonne and Gehling, 2003). Up to 30 taxa have been described from the Mistaken Point beds but study of the 7 most diverse beds reveal 18 taxa with 14 most common (Clapham et al., 2003) (Fig. 2). All three localities display beds with a variety of taxa. The Mistaken Point assemblages have been interpreted as census assemblages showing "snap-shots" of a community structure (Seilacher, 1992), and apparently showing strong similarity to modern epifaunal animal slope communities (Clapham and Narbonne, 2002).

5.4. South Australia

The Ediacara fossil beds in South Australia are particularly valuable as they are younger than the Avalon beds with a more diverse set of taxa. They represent a shallow water depositional setting rather than the deep-water setting of Mistaken Point and are part of, and comparable to, the White Sea Assemblage.

Fossils of the Ediacara biota are confined mainly to facies within the Ediacara Member of the Rawnsley Quartzite, the youngest Neoproterozoic formation in an 8000–15,000 m thick succession that spans the mid and late Neoproterozoic and the early and middle Cambrian in the Adelaide Fold Belt. In the central Flinders Ranges, the fossiliferous Ediacara Member lies 400–600 m below a basal Cambrian disconformity (Gehling, 2000). Lowermost Cambrian strata feature trace and small shelly fossil assemblages of Tommotian age. Depositional thinning toward a western paleo-shoreline put the Ediacara Member just 10–30 m below the Cambrian at Ediacara and Mt. Michael (Jenkins et al., 1983; Jenkins, 1995).

The fossiliferous beds were deposited as storm-sands that inundated normally low energy benthic environments on prograding deltas (Gehling, 2000). They vary from stacked event sands deposited in channels near fair-weather wave base, to thin-bedded sands and silts deposited as waning storm surges below storm wave base. The Ediacara Member varies from 5 to 35 m thick, on the basin margins, up to a maximum of 300 m thick in more distal sections. Although the fossiliferous facies are repeated in four of five parasequences within the Ediacara Member, there is no clear evidence of a significant change in overall composition of the biota between levels (Gehling, 2000). The local assemblages claimed from successive parasequences by Jenkins (1995), are based on specimens from float. The remainder of the 100–1100 m thick Rawnsley Quartzite consists of barren sandstone deposited in shore face and tidal flat environments. The lowest stratigraphic occurrence of Ediacara fossils is in the upper Wonoka Formation, some 500 m below the Rawnsley Quartzite. This level has dense populations of the enigmatic Ediacara index taxon, *Palaeopascichnus*, and some poorly preserved discs and fronds that may be time equivalents of the *Aspidella* beds of the Fermeuse Formation, in SE Newfoundland.

In addition to localities with exposed bedding planes throughout the Flinders Ranges, we have identified 9 beds at South Ediacara and 4 beds near Mt. Michael, where localities offer shallowly dipping fossiliferous outcrops extending over hundreds of square meters. At the field sites, the low angle dip of bedding coincides with low topographic relief such that large areas of bedding surfaces can be exposed with minimum excavation of overburden. Beds must be inverted and re-assembled to allow study of fossil impressions preserved on bed soles. These beds in particular preserve a range of organic structures as well as trace fossils. All beds have body fossils, trace fossils, problematic structures, or organic surfaces or some combination. Body fossil genera include *Dickinsonia* (Fig. 2), *Spriggina*, *Aspidella, Parvancorina* (Fig. 2), *Conomedusites*, *Charniodiscus*, *Tribrachidium*, *Eoporpita*, *Rugoconites*, *Conomedusites*, *Hiemalora*, *Yorgia*, and forms typical of the White Sea assemblage. Trace fossils are also preserved and dominated by simple horizontal traces (Fig. 2) but other more complex types may occur. These beds also reveal a large diversity of bedding plane surfaces and problematic structures that cannot be attributed to physical processes but are clearly organic in origin. Elephant skin (Gehling, 1999) is an example of such a surface feature, but we have at least 6 additional different and distinct types of surfaces that recur commonly occur as patches on bedding planes but may cover large surfaces (square meters). There are also abundant problematic structures (as discussed above) such as “tubes”, “bags” and “tripod impressions”.

Discrete body fossil data from these beds as well as beds in the Flinders Ranges show a degree of heterogeneity between beds both in terms of composition and abundance. Excavation is still underway at Mt. Michael but 8 beds with sufficient abundances allow for comparison with other field localities (Table 1).

6. Comparative bedding plane taphonomy and paleoecology

6.1. Tiering

Tiering is traditionally interpreted as the vertical partitioning of organisms above and below the sediment–water interface. It is comparable to stratification in the tropical rain forests. Tiering is a measure of ecospace utilization. For example, by living at various levels in the water column, animals can tap into different sources of food, nutrients and fluid flow levels. Tiering is a component of the earliest Ediacara communities: the oldest Ediacara fossils, described from the Drook, include the longest (nearly 2 m) Ediacara fossils yet described. Clapham and Narbonne (2002) further described three tiers from the Mistaken Point assemblages: a lower 0–8 cm (above the seafloor), an intermediate 8–22 cm tier and an upper tier that extends as high as 120 cm. Tiers are also apparent in the younger South Australia and White Sea assemblages. Though most fossils reflect low tiering levels, large fronds and stalks demonstrate that complex epifaunal tiering existed throughout Ediacara time. Thus, regardless of

Table 1
Composition of collections from the beds in the Flinders Ranges

Surface	CH 29.14	BathT2	BathT3	CG db	BuG A	MM b3	Es b1	MM b1
N	59	78	41	188	61	217	40	299
Richness	5	4	4	5	5	11	6	2
“*Archaeaspis*”	2							
“Aulozoon”		30						
Arkarua sp. a	45		1					
Aspidella						14	16	297
Charniodiscus					32			
Conomedusites						1		
Dickinsonia costata		4		159	16	147	3	
Dickinsonia lissa						1	1	
Disc 2	3							
Frond1	1							
Intrites						3		
Kimberella			2					
Marywadea					1	2		
Palaeophradmodictya			37			3		
Parvanchorina				2	9	17	1	
Phyllozoon		42						
Rugochonites	8			8			14	
Spriggina					3	7		2
“Striped banana”		2		16				
Tribrachidium			1	3		16		
“Tubes”						6	5	

Mt. Michael and South Ediacara used in Fig. 4.

taxonomic affinities, epifaunal ecospace in the earliest complex multicellular communities was utilized in a manner similar to that today and throughout the Phanerozoic.

6.2. Species richness, evenness and dominance

Ecological systems have two related measures of diversity: richness is a measure of the number of taxa and evenness is a measure of the distribution of individuals among taxa. Both measures are used ubiquitously by ecologists and are significant for understanding and comparing communities. Ediacara assemblages potentially provide the best fossil record for evaluating in situ "community-level" richness and evenness. While, the assemblages may be a combination of live and dead on the seafloor, there is nonetheless only minor time averaging and any transport is easy to identify and thus spatial averaging is not a factor. However, even in Ediacara assemblages, measured richness may not be a true measure of original richness due to a variety of factors including sample size, taphonomy (only those organisms below a mat may be preserved, for example), and lithology. An additional issue unique to the Ediacaran material is the significant amount of problematic material that has not been described. While in some cases, these are common discrete fossils and thus, they are given descriptive "nicknames", such as the "duster", "spindle" and "pectinate" of Newfoundland (Clapham et al., 2004), many more remain unrecorded. Thus, in Ediacaran strata, until these additional fossils are evaluated, richness should be considered a minimum value. Non-standardized richness data collected from bedding planes in Newfoundland, South Australia and the White Sea are comparable and all fall within the range of richness for both modern values and values recorded for Phanerozoic fossil assemblages but at the low end of the range (Fig. 3). Data from Namibia is also included on this diagram and similarly falls within the norm but at considerably lower levels of richness. Importantly, richness data from modern environments and the Phanerozoic is commonly collected as *species* richness, whereas in these diagrams, richness is recorded as genus level and form (e.g. spindle) richness. While these data are not standardized and thus considerable caution should be used in interpretation, it does appear that bedding plane richness decreases from the White Sea assemblages to the Nama assemblages. This is consistent with larger scale evaluations of the three clusters (Gehling et al., 2001).

Rarefied data from Newfoundland and Australia show comparable levels of richness and evenness (Fig. 4). Interestingly, the bulk of the species from Newfoundland are fronds. In South Australia, fronds are not generally preserved and thus, while there are abundant stalks and presumed holdfasts, fronds comprise only one category. Thus, in this case, a taphonomic bias is likely resulting in a lower than would be predicted richness for the South Australia data. That is, the snap-shot may be

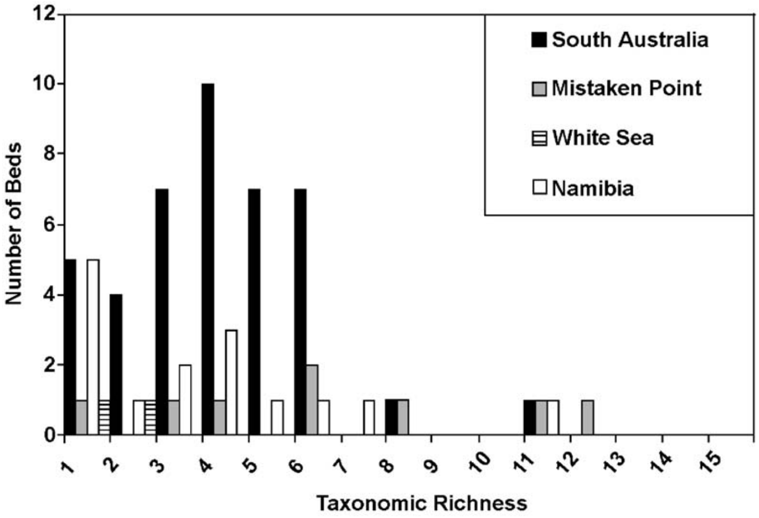

Fig. 3. Histogram of taxonomic richness (including genera and some discrete problematic forms) for a total of 66 bedding surfaces from South Australia, Newfoundland, the White Sea, and Namibia. Richness data are not sample-standardized. Newfoundland data from Clapham et al. (2003) and Gehling (2000). White Sea data are from Grazhdankin (2004). Namibian data are from Grazhdankin and Seilacher (2002) and our own observations. South Australian data were collected by the authors.

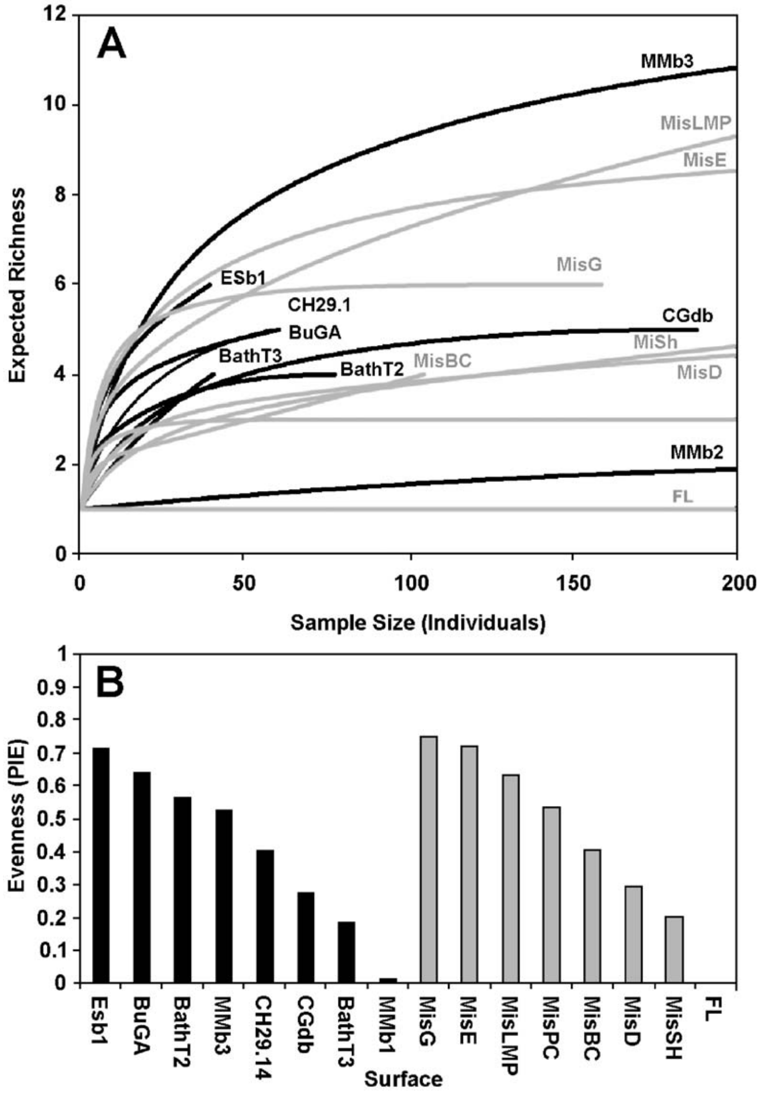

Fig. 4. (A) Rarefaction curves for 16 well-sampled bedding surfaces from Newfoundland and South Australia. Though generally small sample sizes for South Australian bedding surfaces make rigorous comparison difficult, Newfoundland and South Australian faunas appear to have similar ranges of diversity-abundance structure. (B) Range and distribution of evenness values. Eight South Australia and 8 Newfoundland bedding surfaces from (A), ranked by Hurlbert's (1971) PIE. The very low-diversity and low-Evenness Mmb2 (Mt. Michael) and FL (Ferryland) surfaces are highly dominated by *Aspidella*.

missing a significant frond diversity. Additional localities or beds may remedy this situation.

Evenness data is also within the range of modern values but at the low end.

6.3. *Aspidella* beds—populations preserved in situ

Aspidella (Fig. 2) is one of the most common and variously interpreted Ediacara fossils having been interpreted as a mollusk, lichen, fungi, medusoid, gas escape structure, and a concretion. The most accepted interpretation is that it is a holdfast (Gehling et al., 2000). Many discoidal fossils are associated with tubular extensions that either penetrate the overlying bed, or are imprinted on the sole of the bed extending from the disc. Poorly preserved epirelief casts of fronds extending from depressions immediately above discs on bed soles are now well known. Where these discs are named according to various combinations of concentric and radial structures, it is likely that they are all taphomorphs of inflated holdfasts bearing fronds. As yet it is not possible to distinguish the specific characters to separate the holdfasts off frondose taxa. Consequently, these discs have been referred to *Aspidella terranovic* Billings 1872 (Gehling et al., 2000). Buried holdfasts of frondose organisms have a much higher preservation potential than the exposed fronds.

Aspidella occurs in great abundance in all three primary field areas. In Newfoundland Ferryland locality, from large bedding plane assemblages of *Aspidella*, Gehling et al. (2000) described a wide variety of preservational morphs varying from negative hyporeliefs with a raised rim and ridges radiating from a slit to flat disc with a central boss and sharp outer ring to positive hyporeliefs with concentric ornamentation. Similar taphonomic variants are found in South Australia, where the flat morphology is by far the most common. Because *Aspidella* can be a simple disk, it is one of the most common fossils occurring on most every bed. However, there are beds that are completely dominated by *Aspidella* occurring in close association. There may be over 60 discs per square metre, and fossils commonly touch and alter edges.

The distribution of size-frequency data collected from Newfoundland and South Australia is consistent between both localities but the median size is considerably larger in the South Australia material. In all three localities, the size frequency distribution of *Aspidella* is right skewed and is consistent with census populations (Fig. 5). Though the White Sea data were not collected from a single bedding place (Peterson et al., 2003).

Aspidella is a ubiquitous fossil but at least in the South Australia bed from which size frequency data were collected, fossils are preserved in association with organic surfaces as “under” mat structures suggesting that this part of the organism was under the mat in life and that we are casting the underside of a mat and of *Aspidella* holdfasts (Fig. 5).

7. Discussion

7.1. Disparity of forms and increasing community complexity

While species richness and dominance are comparable between the three areas, morphological disparity is not. Ediacara fossils from the Drook Formation in Newfoundland are clearly the oldest reported fossils (Narbonne and Gehling, 2003) and those of the younger Mistaken Point Formation are among the oldest and are generally considered older than those of the White Sea or South Australia. All of these Newfoundland fossils are considered “Rangeomorphs” and are interpreted as a single clade with morphological variations on a theme (Narbonne, 2004). In the Flinders Range, richness and evenness is similar to that of the Mistaken Point communities but the range of morphological forms is

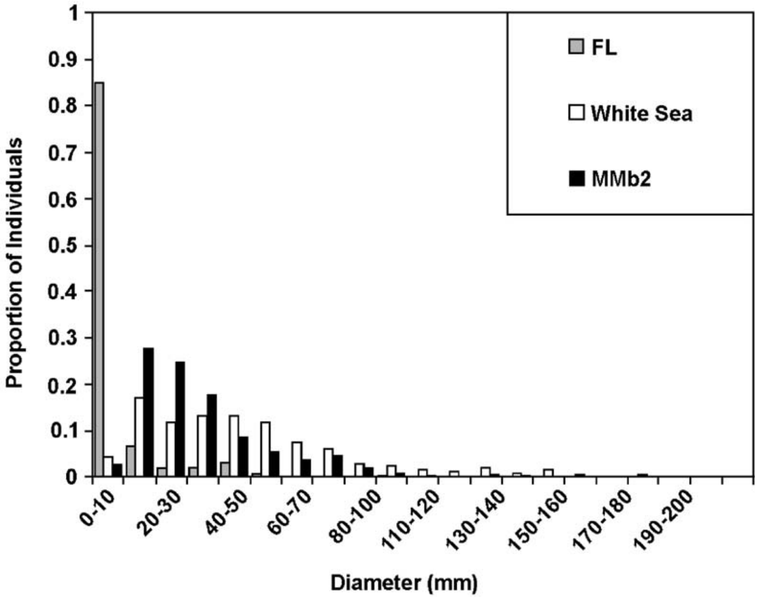

Fig. 5. Size–frequency distributions of *Aspidella* specimens from 3 localities. FL and Mmb2 are single surfaces from Newfoundland and South Australia, respectively, while White Sea specimens come from multiple bedding planes. Highly right-skewed distributions in each case suggest census preservation. FL data from Gehling et al. (2000), White Sea data from Peterson et al. (2003).

considerably greater. Indeed, forms include not only fronds but also "segmented" morphs such as *Dickinsonia* and *Spriggina* and radial forms such as *Rugoconites*. Thus, assuming that an increase in the range of morphologies reflects an increase in ecosystem complexity then the White Sea/Flinders assemblage is more complex than the Avalon assemblage. Both reported diversity and potentially morphological disparity decreases in the Nama group. For example, Seilacher (2003) has interpreted most of the Ediacara fossils of the Nama Group as a single group of sand filled infaunal vendobionts.

7.2. Evidence of mobility for Ediacara-type organisms

While we can reconstruct some aspects of the Ediacara communities one of the most interesting issues is the potential level of mobility among Ediacara organisms. Trace fossil evidence documents that at least there were some mobile benthic bilaterians. But what about the Ediacara organisms themselves? Discussions on the mobility of Ediacara-type organisms were, until recently, based on inferences based on presumed biological affinity. Thus, the water column and sea floor was either relatively teeming with activity (Jenkins, 1992), or the Ediacara-type organisms were immobile and entirely benthic (Seilacher, 1992). Recently, some dickinsonids have been found in direct association with rows of isolated or overlapping imprints that appear to provide evidence of mobility. These have been documented from the White Sea area (Ivantsov and Malakovskaya, 2002; Fedonkin, 2003) and from the Ediacara Member of South Australia (unpublished observation). Furthermore, Dzik (2003) describes and interprets *Yorgia* death tracks from the Zimnie Gory locality in the White Sea. The imprints are preserved in positive relief on bed soles showing that they were originally depressions in the sediment or microbial mat. These imprints may be interpreted as trace fossils, each imprint reflecting the ventral morphology of the organism. By contrast, the body fossil preservation, as is typical for these taxa, is in negative relief on the bed sole. The rows or overlapping series show that the imprints represented stationary phases of an activity different from simple movement over the sediment, which is not likely to leave a trace. Alternative interpretations for these associations as the result of death-struggle or of current transport have been offered (Dzik, 2003); nevertheless, the interpretation as trace fossils seems more compelling. If these are indeed trace fossils it is remarkable that a number of these trace have been found together with their producers, something that is extremely rare for the Phanerozoic. Another Ediacara-type organism, *Kimberella*, has also been found with structures that have been interpreted as trails and radular scratch marks (Gehling, 1996; Fedonkin, 2003). These associations indirectly supports the view that some Ediacara-type organisms were mobile (cf. Gehling, 1991). It is particularly tempting to suggest that several "segmented" taxa with head-like structures, such as *Spriggina*, also were mobile (e.g., Glaessner, 1984; Gehling, 1991). For this to be widely accepted finds of such organisms associated with trace fossils or the demonstration of characters that provide unequivocal evidence for bilaterian affinities probably is necessary. It is worth repeating that a surficial movement in itself is unlikely to leave any trace fossils.

The majority of the more or less radially symmetrical forms are thought to have had limited mobility, regardless of their interpretation as animals or not. For example, *Aspidella*-type discs, whether hold-fasts or representing the full organism, apparently represented a stationary mode of life, which does not preclude that certain movement was possible (see Gehling et al., 2000; Peterson et al., 2003 for different interpretations).

7.3. Heterogeneity between beds

One of the most striking characteristics of Ediacara assemblages is the level of heterogeneity between beds. The origin of this heterogeneity may be due to several taphonomic, environmental or ecological processes. In order to accurately interpret synecology, it is necessary to determine any role that these processes are playing. These processes include:

1) *Taphonomic biases in preservation*: Just as the various Phanerozoic soft bodied fossil lagerstätten represent preservation of only a portion of the present fauna (e.g., Butterfield, 2002, 2003), this needs to be considered here. Various Ediacara forms clearly responded differently to smothering and subsequent degradation (Wade, 1968; Gehling, 1999; Fig. 1). Most taxa preserve in one of four taphonomic classes, as bed-sole casts, external molds, composite molds or, more rarely in South Australia, three-dimensional preservation within a bed. This clearly demonstrates differing grades of tissue construction within the Ediacara biota, in response to burial and decay. It is therefore important to document the type of preservation (top or bottom of bed, concave, convex, composite preservation) for each bed and what signs there are of a microbial mat structures and relation of this to

the fossils. It is important to note that species that had a similar life mode would be found together. Additionally, biostratinomic processes, such as size sorting, may be significant.

2) *Tiering*. While tiering or vertical partitioning is present among Ediacaran communities with respect to the water column, one can also refer to tiering with respect to the vertical partitioning of organisms to the mat. Thus, organisms could live below the mat, within the mat and on the mat (e.g. roughly comparable to undermat miners, mat stickers and mat encrusters of Seilacher, 1999) (Fig. 1; see also Gehling, 1999). This model makes certain predictions about the nature of preservation of these fossils, in particular, overlapping relationships. It also may explain some level of heterogeneity in that only certain levels with respect to a mat may be preserved on a bed. This may be the case with the *Aspidella* bed in South Australia. Casts of *Aspidella* show that these holdfasts were sand-filled but were not overprinted by other densely packed organic debris that strongly patterns this bed. *Aspidella* is therefore interpreted as having been positioned below the mat, while other organisms, like rare specimens of *Dickinsonia* and *Spriggina*, lived on the mat and were preserved as external molds. The fact that a few above-mat organisms were preserved along with the large numbers of *Aspidella* discs, demonstrates that the density of preserved mat texture may obscure fossils, but does not filter them out.
3) *Varying depositional environments*. Grazhdankin (2004) describes 17 beds represented by 4 assemblages. While some fossils cross environmental boundaries, in general fossils occur in recurring distinctive facies-specific assemblages. However, taphonomy plays a further role in the distribution of fossil types. South Australia beds were deposited in similar environmental settings (Gehling, 2000). However, within these settings, small variations in the environment and in particular, energy of deposition is reflected in differences in the composition of bedding plane samples of communities.
4) *Spatial heterogeneity.* Lateral variability in communities and/or community structure can be a result of variable physical processes as discussed above or there can be simply patchiness in organismal distribution as a result of a variety of processes including reproductive strategies and recolonization after storm events. Clearly our limited understanding of the degree of mobility of different Ediacara-type taxa makes it difficult to evaluate the latter. The stratigraphic heterogeneity that we recognize on a bed-by-bed basis may be thus due to lateral heterogeneity. However, both data from Newfoundland (Clapham et al., 2003) and South Australia suggest relatively homogeneous faunal composition on the same bedding plane over distances of 100 m or more.
5) *Succession*. Succession is a quite significant and ubiquitous process operating in modern environments. It is generally thought that it is nearly impossible to test or to document succession in the fossil record because of the obvious difficulties of capturing an ecological community. Ediacara fossil assemblages not only potentially provide such an opportunity but such a process may result in the stratigraphic heterogeneity displayed by Ediacara fossil assemblages. Clapham et al. (2003) document predictable changes in community composition, diversity, spatial pattern and tiering structure in their beds which they interpret as reflecting different successional communities. Early successional communities are characterized by low tiering, high dominance (low evenness) and low diversity. Middle successional communities display the highest diversity and evenness and increasingly complex tiering patterns. Late successional communities have both low diversity and evenness and nonrandom multispecies patterns. Unique taxa not found in other communities are also a component of this community. The successional model here is developed on the basis of beds spread out over 2.5 km and thus, does not invoke true ecological-scale succession.

8. Conclusions

Fossils of the Ediacara biota offer our earliest insight into diverse macroscopic life on this planet. In particular, given the diversity and range of exquisite soft-bodied preservation, the potential for unraveling aspects of the paleobiology and paleoecology is great. Clearly, however, there can be a taphonomic overprint that dictates how complete the assemblage is. Even with this, however, Ediacaran communities demonstrate a diversity, including both evenness and richness that is comparable to both modern and fossil ecosystems and an epifaunal complexity that is comparable with both modern and ancient systems. Future work aimed at understanding and describing the abundant problematica and organic surfaces is, however, necessary before a complete picture of Ediacaran ecosystems can be made.

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