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Paleoecology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland

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Abstract.—Ediacaran fossils at Mistaken Point, southeastern Newfoundland (terminal Neoproterozoic; 565–575 Ma) represent the oldest known animal communities. In contrast to most Phanerozoic fossil assemblages, in which postmortem transportation, bioturbation, and the accumulation of hardparts obscure community relationships, all fossils in the Mistaken Point assemblages were sessile, soft-bodied organisms that show no evidence of mobility in life or transportation after death. Mistaken Point assemblages are spectacularly preserved on large bedding planes as in situ census populations of hundreds to thousands of fossils, recording the living soft-bodied benthic community at the moment it was smothered by volcanic ash. This unique preservation style allows ecological tests routinely conducted in modern communities (e.g., species richness, abundance, ''biomass,'' diversity, and evenness, as well as statistical tests of nearest-neighbor interactions) to be applied to the fossil communities. Observed patterns of community variability are consistent with the theory that Mistaken Point fossil surfaces are ''snapshots'' recording different stages of ecological succession, progressing from communities of low-level feeders (e.g., pectinates and spindles) to frond-dominated communities with complex tiering and spatial structure. The presence of diverse slope communities at Mistaken Point suggests that the deep sea was colonized rapidly during the evolution of complex organisms. Species richness, abundance, and diversity values, as well as levels of intraspecific interaction, all fall within the typical range observed in modern slope communities. These structural similarities imply that ecological processes present in Ediacaran communities at Mistaken Point were strikingly similar to the processes that operate in modern deep-sea animal communities.

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Introduction

The Ediacara biota is a distinctive fossil assemblage of sessile, soft-bodied organisms known from late Neoproterozoic rocks (ca. 575–543 Ma) worldwide (Glaessner 1984; Fedonkin 1992; Jenkins 1992; Narbonne 1998; Martin et al. 2000; Narbonne and Gehling 2003). Ediacaran fossils document a critical interval in Earth history, the transition between the predominantly microbial ecosystems of the Precambrian and the animal ecosystems of the Phanerozoic. Despite their pivotal position in the evolution of life, relatively little is known about the ecology of the Ediacara biota. Ecological interactions between individuals and between species are thought to be limited in Ediacaran communities, although there are very few empirical data to support or contradict this hypothesis. Macropredation appears absent (Glaessner 1984; McMenamin 1986; Seilacher 1992) and other interactions, such as epibiosis, interspecific competition, or mutualism, also were apparently reduced or not present (Waggoner 1998). Different authors have suggested that the Ediacara organisms were heterotrophic suspension feeders (Jenkins and Gehling 1978; Gehling and Rigby 1996; Clapham and Narbonne 2002), chemosynthetic/chemosymbiotic (Seilacher 1992), or photosynthetic/photosymbiotic (McMenamin 1986), although the occurrence of Ediacaran fossils in subphotic deep-water settings implies that those taxa could not be photoautotrophic (Seilacher 1992; Dalrymple and Narbonne 1996; MacNaughton et al. 2000). Study of the Ediacara biota is critical to the understanding of the early evolution of animals and the development of modern-style ecosystems, yet, ex-

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cept for a few local studies, almost nothing is known about the community ecology of these oldest complex ecosystems.

The Mistaken Point area of southeastern Newfoundland (Fig. 1) is a nearly ideal place to study the ecology of the earliest animal communities. The Neoproterozoic succession is thick, richly fossiliferous, and exposed in long, continuous coastal sections. The sections are punctuated by volcanic ash beds, which weather to expose dkm-scale bedding plane surfaces on the tops of mudstone beds. Many of these surfaces contain assemblages of hundreds to thousands of well-preserved Ediacaran fossils, recording a snapshot of the living benthic community at the moment of burial. This lack of taphonomic bias allows outstanding questions of Ediacaran community ecology to be resolved by using techniques routinely applied to modern ecosystems, including parameters of species richness, organism abundance and biomass, and diversity and evenness coefficients (e.g., Mayer and Piepenburg 1996; Gutt et al. 1999). In addition, Ediacaran ecological processes and organism interactions can be accurately assessed with statistical tests describing the spatial pattern of nearest-neighbor distribution (Thrush 1991; Anderson 1992; Campbell 1992; Bellingham 1998; Coomes et al. 1999; Haase 2001). Application of these techniques from modern ecology to the best surfaces through nearly 2.5 km of stratigraphy permits characterization of Ediacaran communities and community processes at Mistaken Point, and evaluation of ecosystem development, through comparison with modern deep-water communities, during the earliest stages of animal evolution.

Mistaken Point Fossils

Soft-bodied Ediacaran fossils were first described from the Mistaken Point area of the southeastern Avalon Peninsula, Newfoundland (Fig. 1), more than 30 years ago (Anderson and Misra 1968; Misra 1969). Subsequent work has documented an abundant and diverse biota occurring on more than 100 bedding planes through nearly 2.5 km of stratigraphic thickness (Anderson and Conway Morris 1982; Narbonne et al. 2001). The abundance of features typical of deep-water turbi-

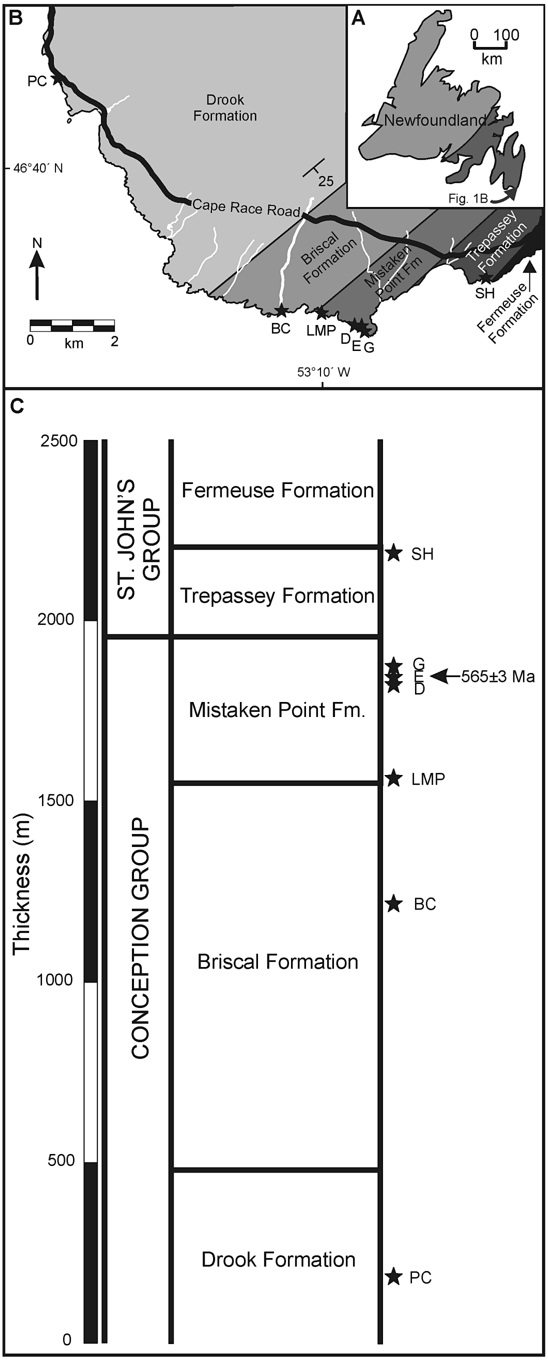

FIGURE 1. A, Location map showing location of study area in the Avalon Zone (dark gray) of southeastern Newfoundland. B, Map of the Mistaken Point area. Studied fossil surfaces are indicated by stars. C, Stratigraphic section of upper Conception Group and lower St. John's Group. Approximate position of surfaces are marked and dated ash beds are indicated by arrows.

dites, coupled with the complete absence of features implying wave influence or emergence, has led previous workers to conclude that the Mistaken Point assemblage lived on a deep-water slope below both wave base and the photic zone (Misra 1971, 1981; Myrow 1995; Narbonne et al. 2001; Wood et al. in press). Radiometric dating of a volcanic ash horizon covering the best-known fossil surface at Mistaken Point yielded a date of 565 ± 3 Ma (Benus 1988) and frondose fossils from the Drook Formation 1500 m lower in the section are probably 10 Myr older (Narbonne and Gehling 2003), suggesting that the Mistaken Point biota is the oldest record of complex, megascopic organisms yet discovered and predates well-known Ediacaran assemblages from Australia, Russia, and Namibia (Narbonne 1998).

The Mistaken Point biota is reported to contain as many as 30 taxa (Anderson and Conway Morris 1982), but in practice only a dozen forms are common (Narbonne et al. 2001). Our detailed study of the seven most diverse fossil surfaces has recorded eighteen taxa (the 14 most abundant are depicted in Fig. 2). With the exception of the discoidal fossil *Aspidella* (Billings 1872; Gehling et al. 2000) and the frondose *Charnia wardi* (Narbonne and Gehling 2003), taxa of the Mistaken Point biota have only been described in general terms, and many have not yet been formally named. Detailed taxonomic studies are in progress, but in the interim this paper follows other studies in utilizing a mixture of formal names of taxa that have been named elsewhere (e.g., *Charnia*, *Charniodiscus*, *Bradgatia*) along with informal but widely and consistently applied names for endemic taxa (e.g., ''spindles,'' ''pectinates,'' ''dusters'') (see also Waggoner 1999; Narbonne et al. 2001).

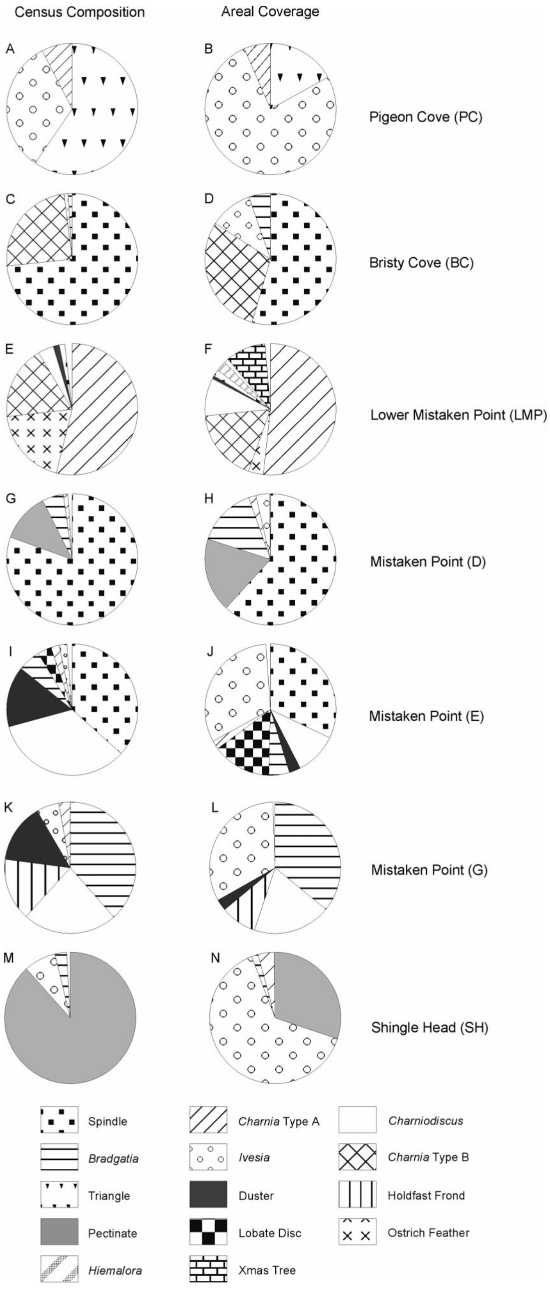

FIGURE 2. Census composition and areal coverage values for Mistaken Point fossil surfaces. Only fossils constituting >1% of the census or areal coverage are shown.

Mistaken Point Surfaces

Coastal sections in the Mistaken Point area are punctuated by literally hundreds of large bedding plane exposures (1–200 m^2 in size) formed by the preferential erosion of weaker volcanic ash horizons. These large surfaces commonly preserve Ediacaran fossils, recording a snapshot of the living benthic community at the instant it was smothered by the ashfall. Seven diverse and well-preserved Mistaken Point assemblages, spanning four successive formations and a stratigraphic distance of nearly 2.5 km, were selected for detailed study (Table 1, Fig. 1). Each contains more than 100 fossils and thus provides a census for statis-

TABLE 1. Summary description of stratigraphic position (below the top of the Trepassey Formation), area studied, smallest feature preserved, number of fossils, and dominant taxa for the studied fossil surfaces. The smallest feature preserved is a taphonomic variable quantifying the finest detail visible on each surface.

Surface	Stratigraphic position	Area studied	Smallest feature preserved	No. of fossils	Dominant taxa
SH	−10 m	47.0 m^2	3.0 mm	370	Pectinate
G	−350 m	7.05 m^2	1.2 mm	162	*Bradgatia, Charniodiscus*
E	−365 m	104.75 m^2	0.5 mm	4188	*Spindle, Charniodiscus*
D	−368 m	63.4 m^2	1.8 mm	1488	Spindle
LMP	−600 m	14.0 m^2	2.0 mm	304	*Charnia A*
BC	−950 m	0.71 m^2	0.3 mm	106	Spindle, *Charnia* B
PC	−2200 m	16.7 m^2	2.0 mm	239	Triangle, *Ivesia*

tical testing and accurate characterization of community attributes.

The studied surfaces were subdivided with a meter-square grid to facilitate data collection. Every fossil was identified and its position recorded within the grid system; each of these records also contains measurements of fossil dimensions and orientation(s). In addition, taphonomic information (e.g., bending, folding, incompleteness, partial preservation due to fracturing or ash cover) was recorded where applicable. Superpositional relationships were also noted, indicating which fossil was preserved underneath in an overlapping pair.

The resulting database contains detailed records for hundreds to thousands of fossils on each surface. However, the Mistaken Point area has been subjected to pervasive tectonic deformation and every bedding plane has undergone significant shortening, altering absolute fossil positions as well as both dimension and orientation values (Seilacher 1999). Deformed positions, dimensions, and orientations were restored to their original values by mathematically removing the apparent bed-parallel shortening in a process called retrodeformation (see Wood et al. in press for a mathematical description of the methodology). All ecological tests were conducted on the retrodeformed database.

How Good Are the Data?

All Mistaken Point taxa represent soft-bodied, sessile organisms. There is little evidence of postmortem transport and no evidence of any infauna (Narbonne et al. 2001), so complicating taphonomic effects, such as spatial mixing of separate populations and time-averaging of living with recently dead material, which are common in Phanerozoic shelly fossil assemblages (Miller 1986; Fürsich and Aberhan 1990; Kidwell 1993; Powell et al. 2002), would not have affected the communities at Mistaken Point. Preservation of the Mistaken Point fossil assemblages as census populations of in situ, entirely soft-bodied, epifaunal organisms, with no evidence of spatial or temporal taphonomic mixing, provides a nearly ideal situation to recreate benthic community paleoecology. Nektonic and planktonic animals would have had a low preservation potential so their abundance (or even presence) in the Mistaken Point biota is uncertain; however, pelagic organisms are typically not included in studies of modern slope benthos either (e.g., Grassle et al. 1975; Smith and Hamilton 1983; Mayer and Piepenburg 1996; Gutt et al. 1999).

Observed differences between communities are indicative of significant biotic patterns only if the variation within a single community is less than that between fossil surfaces. Our qualitative observations of surfaces that crop out in several localities along the sea coast suggested that, although even stratigraphically closely spaced surfaces can differ dramatically in fossil content, lateral variability in the fossil composition of any surface is minimal (Narbonne et al. 2001). The amount and effects of within-surface variation can be quantified by comparing the classic E ''Yale surface'' at Mistaken Point (used for the detailed paleocommunity studies presented below) with a small sample of the E ''Queen's surface,'' also at Mistaken Point but separated from the Yale surface by a 10-m-wide exposure gap, and with the same stratigraphic surface more than 1 km away at Watern Cove. The samples encompassed a range of preservation quality, from uniformly good preservation at E (Queen's) to poorer preservation under thick ash cover at E (Watern Cove). E (Yale) included both high-quality areas and fractured and abraded areas. The effects of preservation quality, which may influence community parameters such as species richness, organism density, and diversity values to varying degrees, will be superimposed upon original compositional differences within the community. Most community parameters were essentially unchanged between differing taphonomic regimes: species richness (10–12 species), diversity (H′ = 1.52–1.68), and evenness (E = 0.61–0.70) are fairly consistent between the three expressions of the E surface. Organism density values showed significant differences that can be directly correlated with quality of preservation, from 31.9 ind/m^2 at E (Watern Cove) to 39.7 ind/m^2 on E (Yale) and 56.5 ind/m^2 on E (Queen's). Lower density on poorly preserved surfaces reflects thick ash cover or abrasion, both of which obscure small specimens. However, areal coverage (a proxy for biomass) was not greatly affected by taphonomy (observed values ca. 10–15%) because preservation quality affects the abundance of small fossils only, which are typically a minor component of community biomass. These results suggest that organism density is strongly correlated with preservation quality in the Mistaken Point assemblages but that other community parameters are not significantly affected by taphonomy and should correspond to meaningful environmental or ecological variables.

Mistaken Point Community Attributes

Mistaken Point communities represent census populations of sessile, surface-dwelling organisms and thus are ideally suited for application of ecological techniques derived from studies of modern communities. Methods used in this study include simple measures of community structure, such as species richness, fossil density, and fossil areal coverage (used as a proxy for biomass), as well as more complex community descriptors such as Shannon diversity and evenness coefficients. Sophisticated statistical tests of nearest-neighbor relationships, for both single populations and the whole community, were used to quantify organism interactions. Descriptions of each of these tests, including a detailed explanation of the methodology of each (where applicable), are presented sequentially in the following sections.

TABLE 2. Summary attributes of Mistaken Point fossil communities.

Surface	Species richness	Fossil density (ind/m^2)	Areal coverage	Shannon diversity	Shannon evenness
SH	6	7.9	3.4%	0.46	0.26
G	6	23.0	6.2%	1.54	0.86
E	12	39.7	12.4%	1.52	0.61
D	8	23.5	11.2%	0.70	0.33
LMP	11	21.7	7.2%	1.31	0.55
BC	4	149.3	6.3%	0.67	0.48
PC	3	14.3	10.7%	0.87	0.80

Species Richness

Species richness ranges from 3 to 12 taxa per locality (Table 2). Because the area surveyed for each surface varied between 0.7 and 105 m^2, and because these variations in sampled area size may strongly influence the observed species richness, we constructed species-area curves (Grassle and Maciolek 1992) by recording the species richness of several (3–8) randomly placed subsamples (1–25 m^2 in size) to investigate the minimum area required to accurately estimate the total species richness of each community (Fig. 3). Species-area curves suggest that the measured species richness for the BC and LMP communities is not an accurate estimate of true species richness but that all other surfaces were adequately sampled.

Fossil Density

Organism density results are difficult to link to ecological or environmental processes because of the potential taphonomic bias against small individuals. Measured organism density in Mistaken Point communities is typically 21–23 ind/m^2 on the LMP, D, and G surfaces, with most other values slightly high-

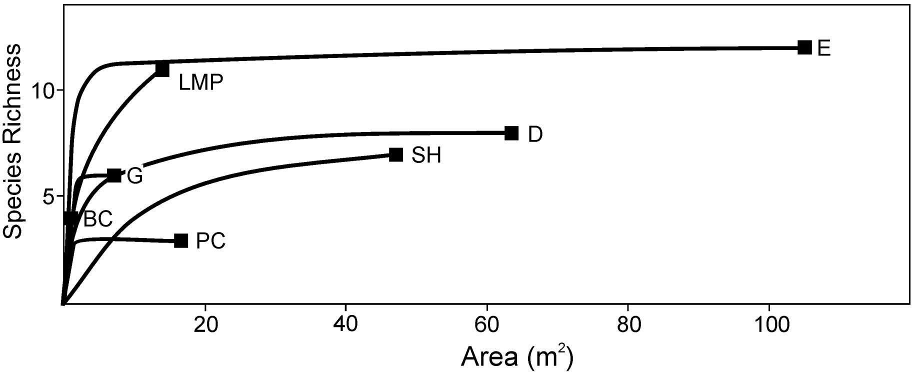

FIGURE 3. Species-area relations for Mistaken Point communities. Species-area curves for each surface were generated by measuring the species richness of randomly placed subsamples.

er (39.7 ind/m^2 on the E surface) or lower (7.9 and 14.3 ind/m^2 at SH and PC, respectively). BC is the only surface displaying significantly anomalous density values (149.3 ind/m^2), resulting from the abundance of small fossils.

''Biomass''

Biomass, as measured in modern ecosystems, cannot be directly calculated from Mistaken Point communities because of uncertainties as to the three-dimensional shapes and material properties of the Ediacaran organisms. Instead, two-dimensional area occupied by the fossils was adopted as a proxy for biomass, allowing approximate comparison of total community areal coverage between Mistaken Point surfaces. Although this is not ideal, it is a far more realistic estimate of biomass than census counts of individuals (irrespective of size) could provide. Fossil areal coverage, expressed as a percentage of total surface area, ranges from 3.4% (SH) to 12.4% (E). Three communities (G, BC, LMP) have relatively low areal coverage, at 6.2%, 6.3%, and 7.2% respectively, whereas the remaining three communities (PC, D, E) have higher areal coverage (10.7%, 11.2%, and 12.4% respectively).

Diversity and Evenness

Lowest diversity is observed on the SH surface, which has a Shannon diversity value of 0.46. The most diverse communities are E and G, with Shannon coefficients of 1.52 and 1.54, respectively. Intermediate diversity values are 0.67 (BC), 0.70 (D), 0.87 (PC), and 1.31 (LMP). Shannon evenness values from Mistaken Point communities span nearly the entire possible range of equitability, from 0.26 (SH) to 0.86 (Gautam et al. 2000:). The seven communities are distributed over the entire equitability range, rather than clustering in discrete groups. Other Shannon evenness values are 0.33 (D), 0.48 (BC), 0.55 (LMP), 0.61 (E), and 0.80 (PC).

Single-Species Spatial Pattern

Methodology.—Many nearest-neighbor techniques for the analysis of spatial pattern exist, although most are derived for sample areas with simple polygonal boundaries (Clark and Evans 1954; Campbell 1992, 1996). Because all six communities (soft-sediment deformation at SH did not permit the original positions of the organisms to be measured accurately) examined at Mistaken Point had irregular boundaries imposed by the edge of preserved outcrop, more-sophisticated statistical tests of spatial pattern are required. Monte Carlo simulation methods are able to compensate for irregular outcrop areas by comparing the observed community spatial pattern to the simulated random spatial patterns of populations with identical boundaries (Coomes et al. 1999). Complete spatial randomness is simulated by a two-dimensional Poisson process, and the cumulative distribution of nearest-neighbor distances from that random population is compared with the observed distribution of distances from the actual population (Coomes et al. 1999).

We modified this procedure slightly for the

E surface, which contains a large area readily recognized in the field as exhibiting lower-quality preservation. The difference in apparent fossil density was incorporated into the model, resulting in a simulated two-density population. This variable-intensity Poisson process provided a more accurate representation of true spatial pattern by reducing the impact of taphonomic effects on the model. We compared the spatial pattern for each taxon by simulating random populations with the same population size in an area with the same boundary shape. On surfaces containing both *Charniodiscus* and dusters, two frondose taxa with indistinguishable discoid bases, the two taxa were combined so that frond bases could be included in the analysis.

Error bounds (95% uncertainty) were estimated by simulating 1000 random populations. Populations with fewer than 20–25 individuals could not be simulated because error bounds on the cumulative distribution of expected nearest-neighbor distances were too great. If the cumulative distribution of observed nearest-neighbor distances passes above the upper boundary of the error envelope, there are significantly more nearest neighbors within a given distance than expected from a random population and the organism has an aggregated spatial pattern (Fig. 4A). Likewise, if the observed distribution passes outside the lower bound of the error envelope there are significantly fewer nearest neighbors than in a random population and the organism has a regular spatial pattern (Fig. 4B).

Results.—Mistaken Point organisms display relatively complex single-species spatial patterns: of 20 taxa examined, 9 were distributed randomly, 8 displayed an aggregated spatial pattern, and 3 had a regular distribution (Table 3). *Ivesia* displayed consistent spatial patterning in different communities (randomly distributed on PC and E), as did *Charnia* Type B (aggregated on BC and LMP). However, most other organisms were aggregated or regular on some surfaces but random on others. *Bradgatia* and the frondose group (*Charniodiscus* and dusters) displayed both aggregated and regular patterns.

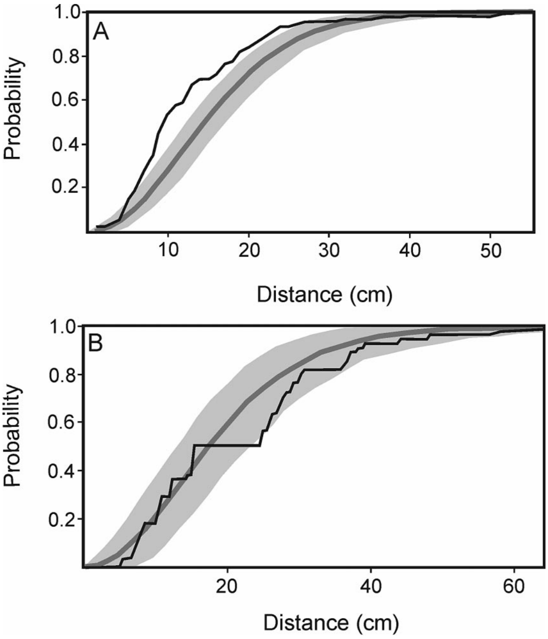

FIGURE 4. A, Cumulative probability distribution for finding a nearest neighbor within specified distance (thick line) for LMP *Charnia* Type A. The 95% error limits for random spatial distribution are indicated by shaded area. Observed distribution (dark line) passes outside of the upper error bound, indicating an aggregated spatial pattern. B, Cumulative probability distribution for finding a nearest neighbor within specified distance (thick line) for G surface *Bradgatia*. The 95% error limits for random spatial distribution are indicated by shaded area. Observed distribution (dark line) passes outside of the lower error bound, indicatinga regular spatial pattern.

Although organisms did not display consistent patterns between surfaces, individual communities tended to have distinctive constituent spatial patterns. For example, the majority (4/7) of species on the E surface are aggregated. Only *Charnia* and the enigmatic lobate forms *Ivesia* and the Lobate Discs are randomly distributed and *Charnia* displayed strong nonsignificant deviation toward aggregation ($p = 0.10$). In contrast, all three organisms examined from the G surface displayed regularity, two significantly and the holdfast fronds at $p = 0.09$. The D surface is unusual in having both aggregated and regularly spaced taxa.

Multispecies Spatial Pattern

Methodology.—Many methods have been derived to model two-species nearest-neighbor interactions in square sample areas (Anderson

TABLE 3. Single-species spatial patterns. Significance levels of aggregation (AGG), regularity (REG), and randomness (Rand) derived from Monte Carlo simulation of spatial pattern. The ''Frondose'' label refers to the grouping of *Charniodiscus* and dusters. The minimum population size for the testing was approximately 20 fossils; taxa with a smaller population are labeled NS (for ''not sufficient''). NP stands for ''not present.''

	PC	BC	LMP	D	E	G
Bradgatia	NP	NS	NP	REG ($p = 0.016$)	AGG ($p < 0.001$)	REG ($p = 0.04$)
Charnia A	NS	NP	AGG ($p < 0.001$)	NS	Rand ($p = 0.10$)	NS
Charnia B	NP	AGG ($p = 0.005$)	AGG ($p = 0.018$)	NP	NP	NP
Frondose	NP	NP	NS	NS	AGG ($p < 0.001$)	REG ($p = 0.05$)
Holdfast stem	NP	NP	NS	NP	NP	Rand ($p = 0.094$)
Ivesia	Rand ($p = 0.21$)	NS	NS	NS	Rand ($p = 0.17$)	NS
Lobate disc	NP	NP	NP	NP	Rand ($p = 0.28$)	NP
Ostrich feather	NP	NP	Rand ($p = 0.14$)	NP	NP	NP
Pectinate	NP	NP	NP	Rand ($p = 0.076$)	NP	NP
Spindle	NP	Rand ($p = 0.14$)	NS	AGG ($p < 0.001$)	AGG ($p < 0.001$)	NP
Triangle	Rand ($p = 0.051$)	NP	NP	NP	AGG ($p = 0.037$)	NP

1992; Dixon 1994; Zou and Wu 1995). Monte Carlo methods, similar to those used by Coomes et al. (1999), allow simulation of multispecies interactions in irregular sample areas. Multispecies Monte Carlo simulation used the same procedure as single-species simulation, but extended to simulate a community with the same number of species and the same-sized populations as the comparison fossil community. For each species, we recorded the identity of each nearest neighbor and tabulated the probability of having a given species as nearest neighbor. Error bounds (95% uncertainty) were derived from 1000 simulated runs. If a species occurs more frequently as a nearest neighbor than expected from two coexisting random distributions then the two species are associated, whereas they are segregated if there are fewer nearest neighbors than expected.

Results.—Only 4 of 64 pairwise nearest-neighbor interactions simulated displayed significant deviation from randomness, both toward segregation. *Charnia* Type A and ostrich feathers both have a segregated distribution in the LMP community. The segregation was two-sided: fewer *Charnia* Type A were neighbors of ostrich feathers than expected, and fewer ostrich feathers were nearest neighbors to *Charnia* Type A. Frondose taxa (*Charniodiscus* and dusters) and spindles also displayed two-sided segregation in the E surface community.

Between-Community Variation

We examined variation in community composition by using cluster analysis (log-transformed data, Bray-Curtis similarity, complete linkage) to classify all Mistaken Point communities, with the three E surface replicates included as separate samples to assess within-community variation. Other clustering methods (e.g., WPGMA, UPGMA) gave similar dendrograms but tended to group the PC and SH surfaces by abundance of *Ivesia* and were not utilized for the final analysis. The resulting cluster dendrogram (Fig. 5) shows that within-community variations for the E surface are much smaller than any between-community differences. This strong similarity further underscores the limited effect of taphonomic

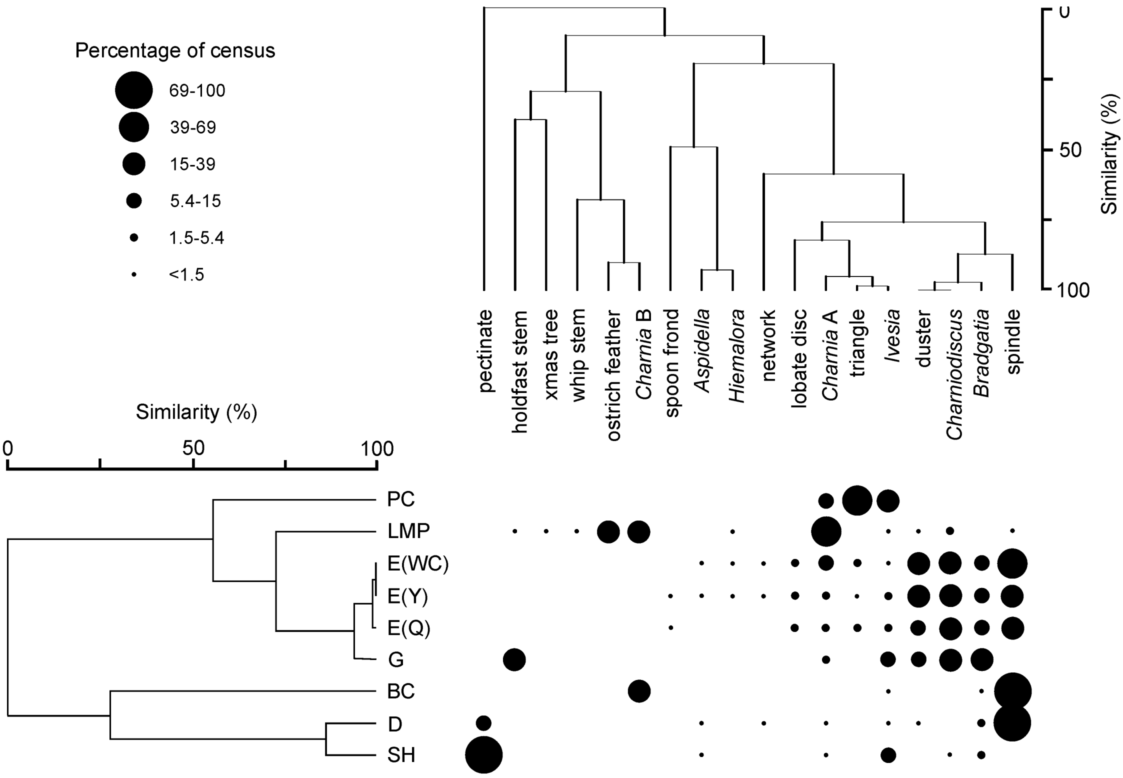

FIGURE 5. Q-mode and R-mode cluster analyses of Mistaken Point communities (complete linkage, Bray-Curtis similarity coefficient).

alteration on community composition. Small within-community variation also suggests that observed between-surface differences are not simply reflections of variability within a single community type. In addition, the uniformity within and between all E surface samples implies that spatial heterogeneity was minimal in Ediacaran communities at Mistaken Point, even at kilometer-scale, in contrast to well-developed patchiness in many modern slope communities (Grassle et al. 1975; Smith and Hamilton 1983; Vetter and Dayton 1999).

Minimal within-surface variation suggests that observed compositional differences between Mistaken Point communities are significant and reflect the ecological or environmental processes that structured those communities. Q- and R-mode cluster analysis (Fig. 5) reveals a fundamental division between two major groupings of communities: frond-dominated communities (G, E, LMP, and to some extent PC) and frond-poor (typically spindle- or pectinate-dominated) communities (BC, D, and SH). Cluster analysis clearly shows groupings of similar communities but does not display environmentally or ecologically mediated gradients in community composition. Such trends are better displayed by ordination techniques that map the relationship between communities in two- or three-dimensional space (Clarke 1993). We chose nonmetric multidimensional scaling (MDS) to compare community similarity because it is a multivariate ordination technique that does not require the data to be normally distributed, making it especially suited to analysis of community abundance data (Field et al. 1982; Clarke 1993). MDS ordination was performed with the PC-ORD software package (McCune and Mefford 1999) and the results are displayed in Figure 6. Although MDS does not rigidly structure variability along the major ordination axes (as in PCA, for example), community trends in ordination space may still be linked to environmental or ecological variables through regression analysis (Clarke

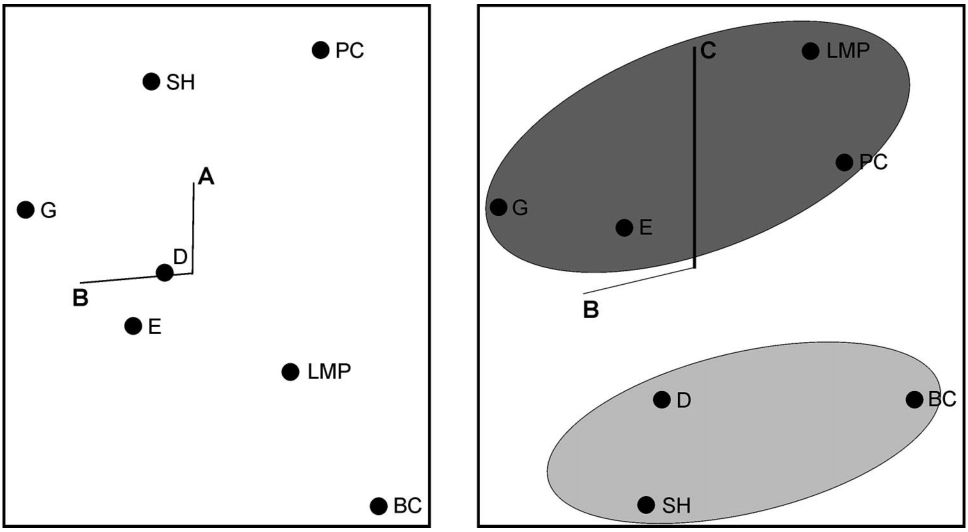

FIGURE 6. Nonmetric multidimensional scaling (MDS) ordination plot for Mistaken Point communities. Stress <0.01 for three-dimensional solution. Regression lines for preservation quality (A), stratigraphic position (B), and proposed ecological succession model (C) are shown. Length of regression line is proportional to the strength of correlation. Shaded ellipses correspond to frond-poor (light gray) and frond-rich (dark gray) groupings from cluster analysis (Fig. 5).

1993). Observed species composition may be controlled by a combination of evolutionary, environmental, and/or ecological factors, although taphonomic effects on species composition must also be considered.

Taphonomic Controls

Before environmental or ecological controls can be assessed as a cause of variation in community composition, the effect of differences in preservation quality must be examined. Taphonomic factors did not significantly affect most community attributes (e.g., richness, diversity) and had a negligible effect on community composition within a single surface. We quantified preservation quality further by measuring the smallest morphological detail typically visible on each surface, which ranges from 0.3–0.5 mm (BC, E) to 3.0 mm (SH). Linear regression of this preservation quality measure for each surface onto the MDS ordination results confirms that taphonomy is only weakly correlated with community variability (regression line A, Fig. 6), suggesting that environmental and/or ecological variables, not preservation quality, are the fundamental controls on community composition.

Evolutionary Controls

Long-term trends in ecosystem composition and structure, resulting from local appearance and disappearance of taxa, may be superimposed on environmental and ecological influences. Local fossil range zones show stepwise appearances and disappearances of taxa, suggesting a possible influence on community structure. Although the Mistaken Point biota spans a stratigraphic thickness of nearly 2.5 km, the grouping of communities in the cluster dendrogram suggests that community composition is only weakly linked to age (Fig. 5). Both clusters contain communities from throughout the stratigraphic succession, implying that local biostratigraphic changes in the biota were not the fundamental control on community composition. However, regression of stratigraphic position (meters below top of the Trepassey Formation) on the MDS ordination plot (Fig. 6) suggests that evolutionary changes did have some influence on community composition. Regression line B shows a moderate correlation with stratigraphic position, with older communities (PC, BC, LMP) occurring near one end of the axis and younger communities (D, E, G, SH) near the other

(Fig. 6). Some community parameters, especially richness and diversity, may also have been influenced by stratigraphic position in the oldest communities, where the regional species pool was smaller (Caley and Schluter 1997; Lukaszewski et al. 1999). It should also be noted that, although there is some correlation between stratigraphic position and community similarity, biostratigraphic changes may not be the proximate cause of variation if stratigraphic position is instead linked to a different environmental or ecological factor. However, the results of cluster analysis and MDS ordination suggest that other environmental or ecological variables were more important in determining overall community structure and composition.

Environmental Controls

Taxa that inhabit modern slope communities often display marked substrate preference (Mayer and Piepenburg 1996; Gutt et al. 1999). However, all seven studied communities were living on silty bottom sediments that are indistinguishable in thin sections, suggesting that differences in community composition did not result from variability in substrate texture and/or composition. Similarly, major differences between the seven diverse Mistaken Point communities do not appear related to resource levels. Four communities (BC, LMP, G, SH) have low areal coverage (''biomass'') values (Table 2), implying that resource levels were low. In addition, the G surface is dominated by regular spatial patterns, suggesting that competition, likely for food, was intense. However, these low-''biomass'' communities do not show strong similarity on the cluster dendrogram (Fig. 5), nor does areal coverage appear as a significant regression trend on the MDS ordination plot. Correlations between areal coverage and species richness or diversity, both of which should vary predictably with resource levels (Wright 1983; Menge et al. 1985; Cosson-Sarradin et al. 1998), are also weak. Some low-''biomass'' communities have low to moderate species richness (BC, G, SH; four to six species), but the LMP community has high species richness (11 species). Likewise, some of these communities have low diversity ($H' = 0.46$ at SH, 0.67 at BC) whereas others are more diverse ($H' = 1.31$ at LMP, 1.54 at G).

Ecological Succession

Important ecological factors in modern communities include predation (Menge et al. 1985; Seitz and Lipicus 2001), competition (Drobner et al. 1998; Menge 2000), and ecological succession (Connell 1978; Visser 1995). Predation can be eliminated as an important structuring mechanism for Mistaken Point communities because there is no evidence for macropredators in any Ediacaran ecosystems (Narbonne 1998). Evidence for intra- or interspecific competition is also limited: regular spatial patterns are rare, as are nonrandom pairwise patterns. In addition, interspecific competition, as an isolated factor, may not be able to influence such disparate community aspects as composition, species richness, diversity, evenness, tiering structure, and spatial pattern.

Ecological succession produces orderly changes in community composition, diversity, spatial pattern, and tiering. Ecological succession is abundantly evident in modern ecosystems (Helm and Allen 1995; Visser 1995; Lichter 1998) and has been inferred from progressive upward changes in Phanerozoic shelly fossil assemblages (Nicol 1962; Walker and Alberstadt 1975; Copper 1988). However, time-averaging in Phanerozoic shelly assemblages may have reduced temporal resolution so that ecological succession may not be resolvable in these records; cases of ''succession'' may instead have been longer-term community replacement mediated by environmental change (Miller 1986). Preservation of Mistaken Point assemblages as census populations of the benthic communities has the disadvantage of presenting them as ''snapshots'' of the living community rather than as a continuous record of the accumulation of hardparts, but the absence of time averaging in these entirely soft-bodied communities provides suitable temporal resolution to recognize ecological succession, if present. The Ediacaran organisms at Mistaken Point inhabited a tectonically active basin, suggesting that the communities may have been affected by occasional disturbances. These disturbances, such as turbidity currents, volcanic ashfalls, and anoxia and/or reduced food supply resulting from slowing or cessation of the contour current (Wood et al. in press), would have resulted in mass mortality of the local biota at random intervals during community development.

If Mistaken Point communities preserve different stages of ecological succession they should also display predictable changes in composition, diversity, spatial pattern, and tiering structure as the conditions become optimized for the growth of different organisms (Walker and Alberstadt 1975; Whittaker 1993). Species composition should change from the pioneer community, characterized by low diversity and evenness, limited tiering, and random spatial patterns (Walker and Alberstadt 1975), through a mixed mid-successional stage, characterized by highest diversity and evenness (Walker and Alberstadt 1975), increasing tiering complexity (Helm and Allen 1995; Lichter 1998), and more nonrandom spatial patterns from competitive exclusion and preferential colonization of empty spaces (Bellingham 1998), to the climax community, characterized by high or slightly decreased diversity (Walker and Alberstadt 1975; Clebsch and Busing 1989), lower evenness values from enhanced competitive exclusion (Death 1996; Drobner et al. 1998), and the greatest tiering and spatial pattern complexity (Helm and Allen 1995; Bellingham 1998; Lichter 1998). The following section will investigate whether the ‘‘snapshots’’ represented by the Mistaken Point fossil surfaces might reflect different stages in this idealized succession model.

Early Succession.—Early successional (‘‘pioneer’’) stages typically display low diversity and highly uneven species abundances, with minimal tiering and spatial pattern complexity. Community parameters measured from BC, D, and SH communities are most similar to the values expected from early stages in ecological succession. Diversity is low ($H' = 0.46–0.70$), as is evenness ($E = 0.26–0.48$). Both BC and D have random multispecies spatial patterns (spatial patterning at SH could not be studied) and tiering is present only in the D surface community. The extremely low diversity and evenness at SH suggest it could represent an earlier, pioneer community with BC and D recording slightly later stages in succession. The grouping of BC, D, and SH communities as potential pioneer stages is supported by the cluster dendrogram, which, despite their occurrence at different stratigraphic levels, groups those communities together as one of two fundamental clusters (Fig. 5).

Middle Succession.—Mid-succession communities typically have the highest diversity and evenness, as well as displaying increasingly complex tiering and spatial pattern. The G surface community has high diversity and evenness values, with complex tiering and random multispecies spatial patterns, and is most consistent with mid-successional position. The E surface community is similar to the G community in terms of diversity and tiering, but it has lower evenness and contains nonrandom multispecies spatial interactions, possibly indicating greater similarity to a later successional position. The PC community is difficult to place in the succession, owing to its low stratigraphic position and corresponding depauperate fauna. The diversity value of 0.87 is more similar to an early successional stage but the high evenness value (0.80) is more consistent with a mid-successional position, similar to the G surface community.

Late Succession.—The LMP community is the most consistent with a late succession stage, having both lower diversity and evenness than the potential mid-succession communities (E, G), and nonrandom multispecies patterns. The community has a unique species composition, with a much greater proportion of frondose taxa, distinguishing it from the less frond-rich E and G communities. The LMP community also contains unique meter-tall organisms not found on any other surfaces in the study area (Clapham and Narbonne 2002).

Proposed Ecological Succession Model.—The fundamental division between the probable mid- to late-succession PC, LMP, E, and G communities and the pioneer-like BC, D, and SH communities is well supported by cluster analysis (Fig. 5). The proposed succession pattern (earliest SH to early BC/D to middle PC/E/G to late LMP) was examined by coding each stage with an integer value (1 through 4) and performing regression analysis in MDS

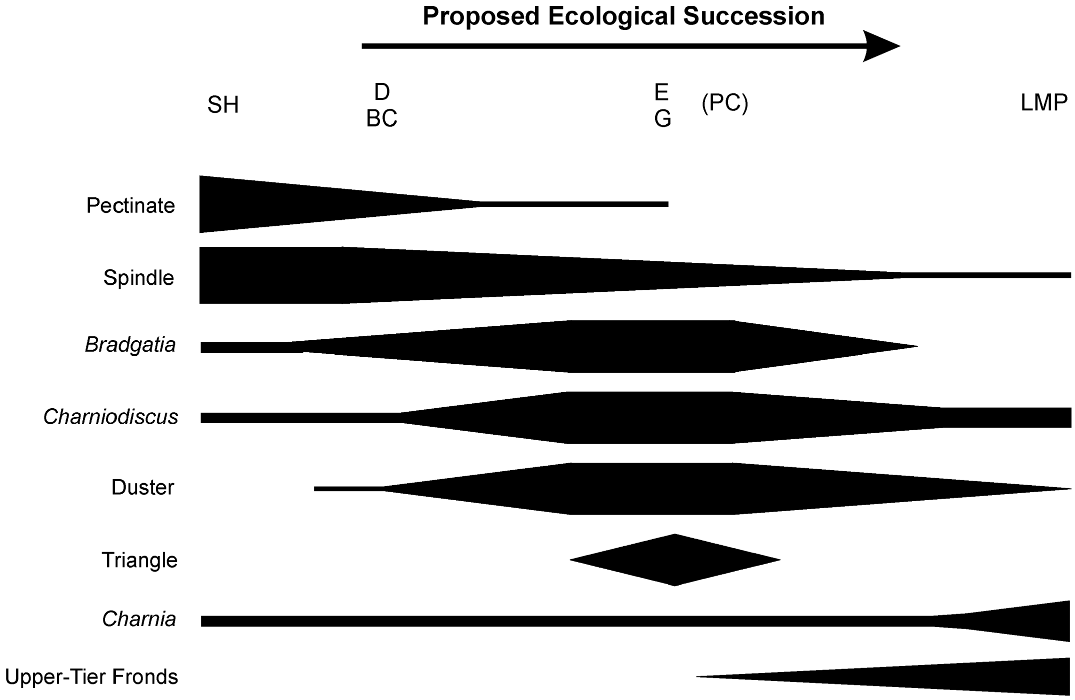

FIGURE 7. Approximate trends in species composition between different Mistaken Point communities. Position of communities along horizontal scale is based on community parameters, cluster analysis, and MDS ordination and parallels the proposed ecological succession model.

ordination space. The correlation between a priori successional stage (1 through 4) and community variability is strong (regression line C, Fig. 6).

The trends in community species composition are consistent with the proposed ecological succession model (Figs. 7, 8). The general trend through succession appears to have been the replacement of flat-lying organisms with upright, frondose organisms, possibly as sediment became increasingly stabilized by microbial mat. Early successional stages (SH, BC, D) may have been dominated by pectinates and/or spindles, whereas intermediate stages (E, G) were characterized by abundant *Charniodiscus*, dusters, and *Bradgatia*. The proposed mid-succession PC community did not contain these organisms because it predated their first appearances; however, it is dominated by the triangle form, which was typical of other mid-succession assemblages (E surface). The potential late-stage community (LMP) was completely dominated by frondose organisms: small fronds such as *Charnia* Type A and ostrich feathers largely replaced spindles and *Bradgatia* in the lower tiers, and the uppermost tier was occupied by rare meter-tall forms such as the whip stem and Xmas tree (Clapham and Narbonne 2002).

If the communities reflected different successional stages, trends in species composition (Fig. 7) should result in predictable changes in multispecies interactions (where present) as early species were replaced by new colonizers (Bellingham 1998). If succession was based on a tolerance model, in which the community changed through progressive displacement by species adapted to lower resource levels (Miller 1986), later colonizers should have preferentially settled in locations where preexisting species were less densely packed. Observed nonrandom multispecies spatial patterns are consistent with a tolerance model of succession. Ostrich feathers (interpreted late-stage colonizers of the lower tier) in the LMP community tend to be segregated from *Charnia* Type A, which occurs at every stage of succession. On the E surface, mid-succession frondose forms (*Charniodiscus* and

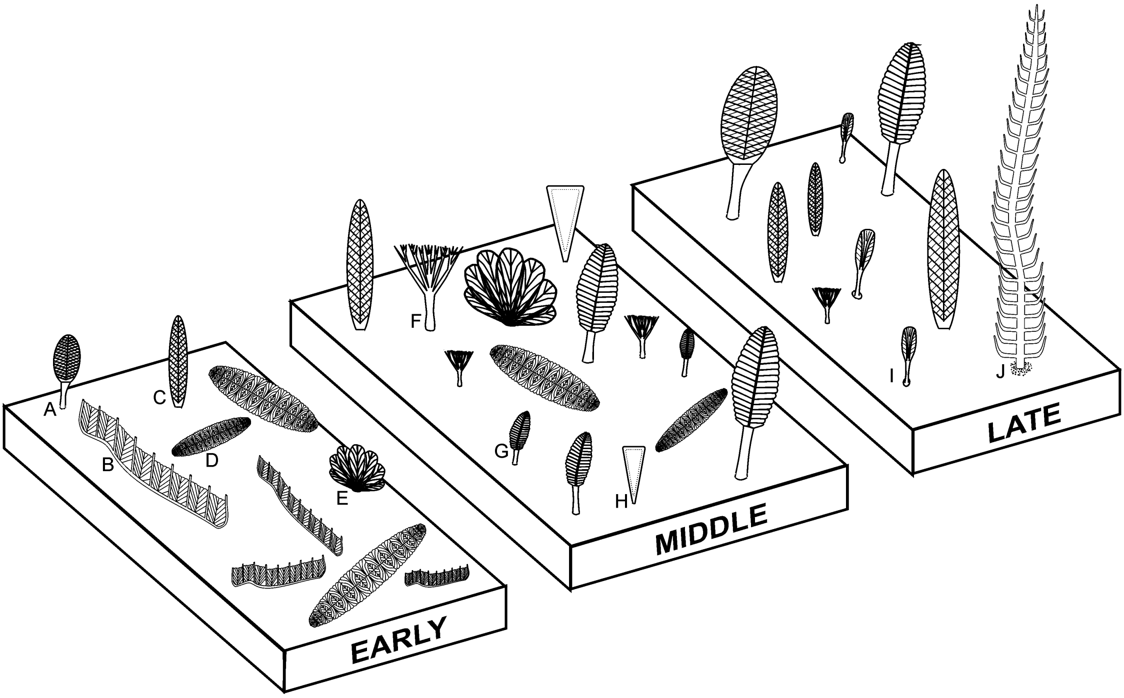

FIGURE 8. Diorama illustrating idealized progression of communities during ecological succession. A, *Charnia* Type B. B, Pectinate. C, *Charnia* Type A. D, Spindle. E, *Bradgatia*. F, Duster. G, *Charniodiscus*. H, Triangle. I, Ostrich feather. J, Xmas tree.

dusters) are segregated from early-succession spindles.

Although the preservation of the Mistaken Point communities as census populations makes it impossible to prove conclusively that between-community differences result from ecological succession, the succession model is internally consistent and agrees with observed variation in community structure. The proposed succession model is well supported by cluster analysis and MDS ordination, and corresponds well to changes in diversity, evenness, spatial pattern complexity, and tiering structure. Species composition trends and interspecific interactions also vary predictably in correspondence with the proposed model.

Comparison with Modern Communities

Mistaken Point fossil assemblages provide the opportunity to study the relationships between the early evolution of animals and the evolution of animal ecosystems. Because communities at Mistaken Point preserve census populations of the benthic megafauna living in a slope community, they can be compared directly with modern bathyal megafaunal communities. Comparisons with Phanerozoic shelly fossil assemblages are less secure because of time-averaging and the taphonomic bias against soft-bodied organisms inherent in those assemblages. If complex community structure is an inherent property of assemblages of complex animals, the structure (richness, diversity, spatial patterning) of Mistaken Point communities should be similar to that of equivalent modern communities. If, however, complex communities are a feature that evolved gradually during early animal evolution, then Mistaken Point may show lower species richness, lower diversity, or less developed spatial patterns than modern counterparts.

Species richness, Shannon diversity indices, and spatial patterning from Mistaken Point communities were compared with values from modern bathyal megafaunal communities. In the comparison studies of modern slopes, megafauna refers to organisms visible on photographic transects and generally in-

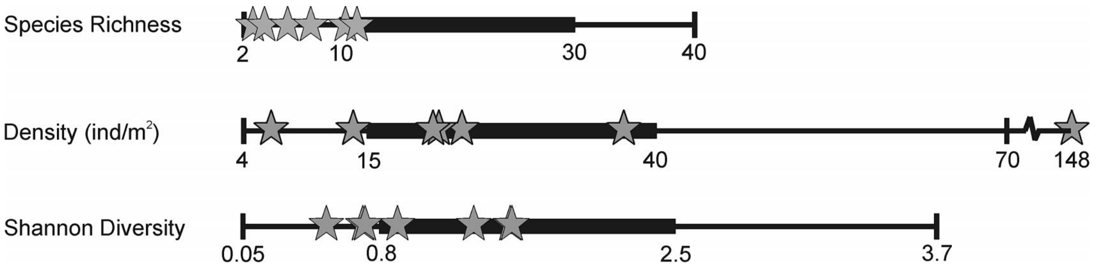

FIGURE 9. Comparison of species richness, average fossil density, and diversity values from Mistaken Point communities (stars) with typical (filled rectangle) and extreme (solid line) range from modern slope communities of epibenthic megafauna.

cludes all epifaunal organisms larger than 0.5–3 cm, depending on photographic resolution, a size limit that is comparable with the taphonomically controlled minimum visible size at Mistaken Point. Only photographic studies were used for comparison purposes because trawl samples typically include infauna, which are far more abundant than epifauna in modern settings (Grassle et al. 1975), and which were absent from Ediacaran communities at Mistaken Point.

Species richness varies greatly on the modern slopes, with typical values between 10 and 30 species, for areas of ca. 10–100 m^2, and a maximum range of 2 to 40 species (Grassle et al. 1975; Smith and Hamilton 1983; Mayer and Piepenburg 1996; Gutt et al. 1999). Mistaken Point communities fall within the typical range of modern communities (Fig. 9), although in general they are moderately species-poor with a maximum of 12 species per community. Mistaken Point communities also fit well within the observed range of Shannon diversity coefficients from modern communities (Fig. 9). Shannon diversity can be as low as 0.05 (Grassle et al. 1975; Smith and Hamilton 1983) or as high as 3.7 (Mayer and Piepenburg 1996) but typically ranges between 0.8 and 2.0 (Gutt et al. 1999), comparing well with Mistaken Point communities ($H' = 0.5$–1.5). Although fossil density measures at Mistaken Point are strongly confounded by taphonomic bias, density seems to be equal to or greater than density values observed on modern slopes. Values as high as 70 ind/m^2 have been reported from modern settings (Gutt et al. 1999), but typical values range from 15 to 40 ind/m^2 (Smith and Hamilton 1983; Mayer and Piepenburg 1996). Observed values in Mistaken Point communities are as low as 8 ind/m^2 and as high as 148 ind/m^2 (Fig. 9), although evidence from the E surface suggests that typical density values for Mistaken Point communities may have been 50–150 ind/m^2, much greater than the animal density found on modern slopes.

Spatial patterns, especially multispecies distributions, are thought to indicate higher-level community structuring including intra- and interspecies interactions. Random single-species patterns are most common in some slope communities (Grassle et al. 1975), whereas aggregation or regularity predominate in others (Smith and Hamilton 1983). Of 211 single-species distributions examined by Mayer and Piepenburg (1996), 81 showed significant aggregation and the other 130 were random. Mistaken Point communities also displayed significant levels of spatial patterning: more than one-half of single-species distributions deviate from randomness, with aggregation more common than regularity. Multispecies spatial patterns are rare at Mistaken Point, with 60 of 64 pairwise interactions conforming to a random distribution, but the frequency of multispecies patterning in the modern deep sea is poorly understood, making it difficult to determine if Mistaken Point communities are in fact less complexly structured.

Mistaken Point communities fall within the typical range of species richness and diversity for modern marine epibenthic communities and displayed similar levels of single-species spatial patterning. Fossil density is consistently higher than in modern slope communities but interspecies interactions may have been less common. These results imply that the structural organization of the oldest animal communities at Mistaken Point was similar to community structure of modern slope communities.

Conclusions

Mistaken Point communities display significant between-community variation, likely resulting from ecological processes with superimposed evolutionary and environmental effects. Modern communities are influenced by a myriad of interrelated factors, including nutrient levels, disturbance frequency, environmental heterogeneity, competition, predation, and ecological succession, to name a few. Some of these controls, such as predation, were absent from Ediacaran communities at Mistaken Point. In addition, the homogeneous nature of the E surface community, even at localities over 1 km apart, suggests that environmental heterogeneity was negligible. Modern communities display extreme variability over small and intermediate scales (Grassle et al. 1975; Mayer and Piepenburg 1996), in contrast to the spatially uniform community structure observed at Mistaken Point. Major community variability is consistent with control by ecological succession, and there is also evidence for intraspecific competition, and possibly limited interspecific segregation, in several communities. The presence of these complex controls implies that Mistaken Point communities were largely structured by the same set of parameters that are active in modern communities.

Although this study does not constrain the affinities of component organisms, it does allow speculation on their environmental tolerances and reproductive strategies. For example, the abundance of random and regular spatial distributions in Mistaken Point communities implies that the constituent organisms had a dispersal phase in their life cycle. The global distribution of *Charniodiscus*, *Charnia*, and *Hiemalora* further suggests that at least some Edicaran taxa may have possessed a teleplanic larva.

The census populations at Mistaken Point preserve diverse communities that inhabited the deep slope during the Neoproterozoic. The presence of a diverse slope biota at Mistaken Point suggests that the deep sea was colonized rapidly at an early stage of animal evolution. Mistaken Point communities are significantly richer than the deep-water biota from northwestern Canada (Narbonne and Aitken 1990) and England (Ford 1999), and similar studies of these localities are necessary to fully elucidate the paleoecology of Ediacaran slope environments. Similarly, shallow-water Ediacaran assemblages such as those in Australia, the White Sea, and Namibia are markedly different in composition from those at Mistaken Point, and quantitative studies are needed to determine how these differences affected their ecological structure.

As a final conclusion of this study, it is interesting to note that the earliest complex communities in the fossil record have structural attributes strikingly similar to those of modern counterparts. Species richness, organism abundance, and diversity values, as well as levels of spatial patterning, all fall within the norms of modern epibenthic slope communities. Only interspecies interactions appear less common. These community similarities suggest that, although the taxonomic affinities of Ediacaran organisms are unknown, they had many of the same ecological responses as present-day animals.

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