Ediacaran epifaunal tiering

M.E. Clapham
G.M. Narbonne ⎫ Department of Geological Sciences, Queen's University, Kingston, Ontario K7L 3N6, Canada

ABSTRACT

Epifaunal tiering, the subdivision of vertical space within a community, is a fundamental attribute of Phanerozoic suspension-feeding communities. This paper documents tiering, including the presence of meter-tall organisms, in Neoproterozoic Ediacaran communities. Ediacaran tiering was studied from three exceptionally preserved deep-water communities at Mistaken Point, Newfoundland, which contain in situ census populations of hundreds to thousands of organisms. Tiering consists of overlapping populations of dominant organisms and is characterized by gradational, rather than abrupt, tier boundaries. At least three tiers are apparent: a lower level 0–8 cm above the seafloor, an intermediate level between 8–22 cm above the seafloor, and an upper level that extends as high as 120 cm. Tier boundaries are relatively consistent between communities, but the constituent organisms in each level are variable, suggesting that some Ediacaran taxa could fill different tiers interchangeably. Development of a tiered epifaunal structure is consistent with suspension feeding or absorbing dissolved nutrients directly from seawater. Despite the common occurrence of tall organisms, all communities share a similar population structure in which biomass is concentrated in the basal 10 cm above the seafloor. Comparison with shallow-water Ediacaran localities suggests that the observed tiering structure is typical of Ediacaran communities. Ediacaran tierers also show the fundamental subdivision between organisms and/or colonies that fed along their entire length and those that developed a specialized feeding apparatus, implying that the features of Phanerozoic tiered skeletal ecosystems were first initiated in soft-bodied communities in the late Neoproterozoic.

Keywords: Ediacaran, Neoproterozoic, Newfoundland, paleoecology, tiering.

INTRODUCTION

Epifaunal tiering, the development of a vertically stratified community structure above the seafloor, is commonly adopted in extant marine communities as a biological solution for resource partitioning. Tiering has been inferred from numerous studies of Phanerozoic shelly fossil assemblages, and complex tiering of skeletal organisms is generally thought to have originated during the Ordovician with the evolution of large, stalked crinoids (Bottjer and Ausich, 1986). Tiering in soft-bodied Ediacaran ecosystems has previously been discussed only from a theoretical perspective based on published heights from the literature (Narbonne, 1998; Ausich and Bottjer, 2001). This paper is the first to fully document tiering structure from individual Ediacaran communities.

The Ediacara biota is an assemblage of soft-bodied organisms that were globally distributed during the late Neoproterozoic (Narbonne, 1998). The affinities of the Ediacara biota are controversial (see Runnegar, 1995; Narbonne, 1998, and references therein), but it is most commonly regarded as dominated by cnidarian-grade animals and/or extinct groups possibly allied with the Cnidaria (Buss and Seilacher, 1994). Complex Ediacaran fossils were first described from the Mistaken Point area in southeastern Newfoundland (Fig. 1) by Anderson and Misra (1968). Subsequently, hundreds of fossil-bearing surfaces, spanning a stratigraphic interval of more than

3 km, have been found in this area (Narbonne et al., 2001). Taxonomic study of these assemblages is ongoing; several important taxa that have not yet been formally described are referred to in the literature by using consistent but informal terms (e.g., spindles, pectinates). Whereas most Ediacaran assemblages reflect shallow-water conditions (Narbonne, 1998), the turbiditic nature of the sediments at Mistaken Point, containing abundant slumps and debris flows but no wave-generated structures, suggests that it is one of the few deep slope localities, occurring well below both wave-base and the photic zone (Misra, 1971; Landing et al., 1988; Myrow, 1995; Narbonne et al., 2001). Fossil assemblages at Mistaken Point were instantaneously buried beneath volcanic-ash layers, preserving census populations of in situ communities (Seilacher, 1992). The ash was dated as 565 ± 3 Ma (U-Pb on zircons, Benus, in Landing et al., 1988), implying that Mistaken Point assemblages are the oldest known complex animal communities.

Tiering has long been recognized in terrestrial forest communities, where height stratification results from competition for light (Cannell and Grace, 1993). Studies of subtidal kelp forest communities suggested that stratification in the marine realm could also result from competition for light (Foster, 1975). Epifaunal tiering was also observed in paleontological studies, mainly of Paleozoic suspension-feeding, skeletal organisms, where particulate food,

not light, is the limiting resource (Lane, 1963; Brett and Liddell, 1978; Watkins, 1991).

Epifaunal tiering in filter-feeding communities develops as a means of resource partitioning in an environment in which sessile organisms receive nutrients from horizontally moving currents (Bottjer and Ausich, 1986). A distinct velocity gradient forms within the bottom current, so that epifaunal organisms can take advantage of faster water flow, and therefore greater feeding capacity, by growing higher in this hydrodynamic boundary layer. In addition, by becoming taller than its neighbors, an organism can gain a distinct competitive advantage by feeding from a previously untapped nutrient source (Bottjer and Ausich, 1986).

Tiering was best developed in the Paleozoic (post-Ordovician) and the early Mesozoic, when skeletal epifaunal communities were stratified into four levels: 0–5 cm, 5–20 cm, 20–50 cm, and 50–100 cm above the substrate (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986). The relative abundance of organisms in
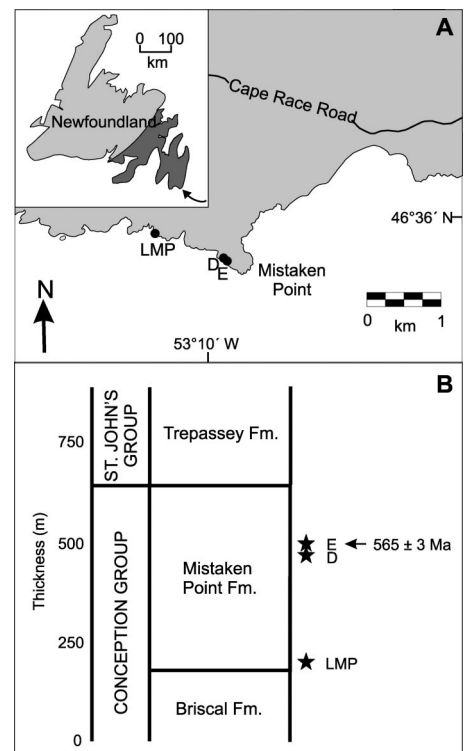

Figure 1. Occurrence of complexly tiered Ediacaran communities at Mistaken Point, Newfoundland. A: Location map (Avalon terrane is shaded). B: Composite stratigraphic section, showing position of Lower Mistaken Point (LMP), D, and E fossil surfaces and ash dated as 565 ± 3 Ma.

each tier was not presented, although studies from well-preserved Silurian communities show that <10% of suspension-feeding species were taller than 10 cm (Watkins, 1991; Taylor and Brett, 1996). Two food-gathering strategies were adopted by Phanerozoic primary tiering organisms: colonial tierers (e.g., tabulate corals and bryozoans) gathered food along their entire length, whereas solitary tierers (e.g., crinoids) developed a specialized feeding apparatus suspended above the seafloor (Bottjer and Ausich, 1986).

Tiering was not well developed in Cambrian and Early Ordovician skeletal epifaunal communities (Ausich and Bottjer, 1982, 2001). Studies of tiering in Cambrian Lagerstätten have not been carried out, but the presence of tall filter-feeding organisms in the Burgess Shale (Conway Morris, 1986, 1993) and Chengjiang (Chen and Zhou, 1997) biotas suggests that detailed studies of tiering among soft-bodied filter-feeders could be fruitful.

EPIFAUNAL TIERING AT MISTAKEN POINT

Ediacaran assemblages at Mistaken Point (Fig. 1) provide a superb natural laboratory to investigate the ecology of early animals. The three largest, most densely populated, and diverse fossil surfaces in the Mistaken Point Formation, the D, E, and Lower Mistaken Point surfaces, were selected for detailed study of tiering relationships. All identifiable complete fossils on each surface (250–2800 fossils) were measured. Height was determined by measuring the combined frond and stem length of frondose taxa and the total length of other upright organisms (see Seilacher, 1999; Narbonne et al., 2001). Because the region has undergone tectonic deformation, all measured fossil heights were mathematically retrodeformed to remove the effects of cleavage-related shortening and restore the original height of the living organism (see Seilacher, 1992). Spindles were dominantly horizontal on the seafloor; however, taphonomic evidence suggests that they had a height above the substrate approximately equal to half of their width (J. Gehling, 2001, personal commun.). As with Phanerozoic and living benthos (Okada and Ohta, 1993), it is probable that at least some of the frondose taxa of the Mistaken Point Formation were oblique to the seafloor during life (see also Seilacher, 1992). If so, the measured organism length does not provide an absolute value for height above the seafloor, but does provide a measure that can be directly compared with Phanerozoic communities in which tiering height was also measured from the maximum length of the fossil.

Tiering is well developed on all three of the fossil surfaces (Fig. 2). On these bedding planes, epifaunal space is subdivided into
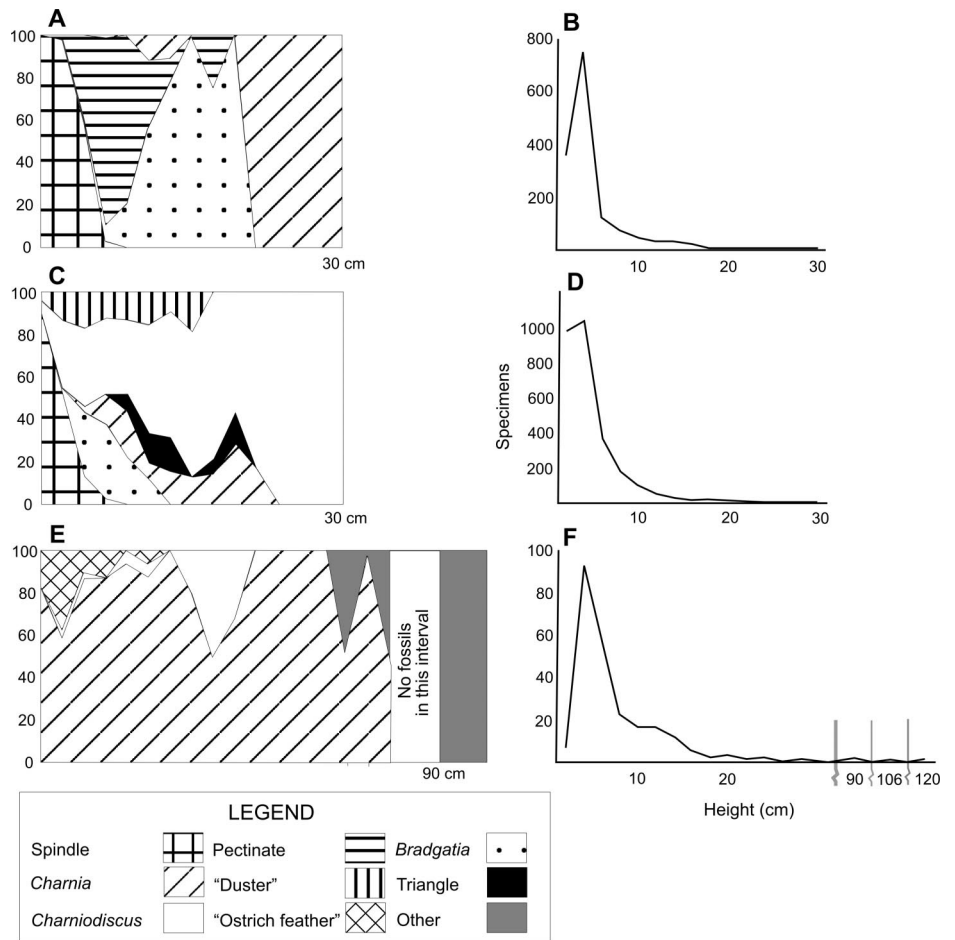

Figure 2. Cumulative-percentage species composition of each tier and total-population size-frequency distribution for each surface studied at Mistaken Point. A and B: D surface. C and D: E surface. E and F: Lower Mistaken Point surface.

overlapping regions characterized by one or several dominant organisms. Dominance was quantified by the percentage abundance of complete fossils in each 2 cm height class (Fig. 2). Representative examples of each of the main fossils in the Mistaken Point Formation are illustrated in Figure 3.

D Surface

The D surface species composition (Fig. 2A) displays the gradation of forms above the seafloor that is typical of Ediacaran communities at Mistaken Point. There is a progressive domination of specific taxa with increasing height, beginning with the lowest level of spindles (A in Fig. 3) at 0–8 cm above the seafloor. The next epifaunal level is dominated by pectinates (E in Fig. 3) between 4 and 14 cm, and *Bradgatia* (F in Fig. 3), which occurs at heights of 8–22 cm. The upper epifaunal level, between 22 and 30 cm, is exclusively populated by *Charnia* (D in Fig. 3). The total-population height distribution (Fig. 2B) has a maximum at 4 cm and is strongly left skewed, so that, although heights to 30 cm are observed, nearly 95% of all specimens are <10 cm tall.

E Surface

The E surface displays a similar, but more complex, pattern of overlapping species (Fig. 2C) to that observed on the D surface. Species that occupied a single level on the D surface may occupy the same level, a different level, or multiple levels on the E surface. In addition, more unique forms are present on the E surface. Spindles again dominate the lowest level from 0 to 8 cm height. Intermediate levels are composed of gradational populations of *Bradgatia* (6–14 cm), *Charnia* (8–22 cm), and triangles (G in Fig. 3; 10–20 cm). Duster forms (H in Fig. 3) occur at all heights up to 16 cm and *Charniodiscus* (C in Fig. 3) dominates most height classes, especially above 20 cm. As with the D surface, organism lengths are strongly skewed to short heights, with a peak at 4 cm and 95% of specimens <10 cm tall.

Lower Mistaken Point Surface

The Lower Mistaken Point surface contains the simplest tiering structure, although the general pattern is the same as that observed on the previously described surfaces. The community is composed almost entirely of
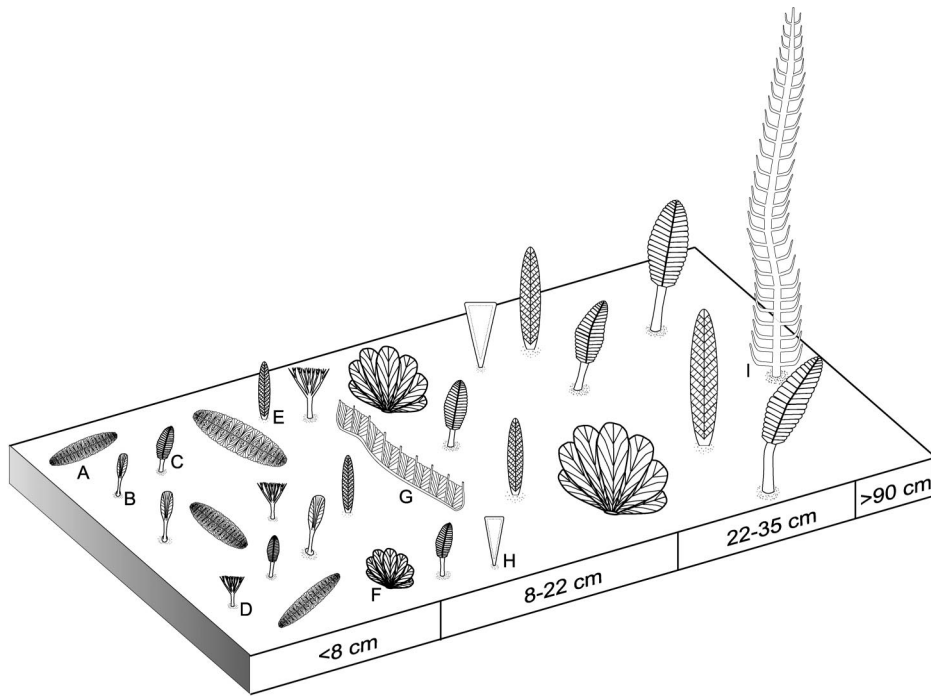
Figure 3. Diorama of composite Mistaken Point community, showing tiered epifaunal structure. A: Spindle. B: Ostrich feather. C: *Charniodiscus*. D: Duster. E: *Charnia*. F: *Bradgatia*. G: Pectinate. H: Triangle. I: Xmas Tree.

frondose taxa; only three spindles are present at the lowest levels. *Charnia* dominates most levels up to 35 cm. The non-*Charnia* population is subdivided between "ostrich feathers" (B in Fig. 3), which are present at low heights (0–10 cm), and *Charniodiscus*, which is more abundant at higher levels (14–22 cm). The population structure has a peak at 4 cm height and is dominated by small specimens (80% are <10 cm tall). However, this surface differs from the D and E surfaces in the presence of three rare forms (such as the "Xmas tree"; I in Fig. 3) at heights of 90–120 cm above the seafloor.

Tiering Structure

All three surfaces display a consistent pattern of overlapping dominant organisms, although the faunal composition differs considerably. Boundaries between each of the levels are typically gradational (e.g., Fig. 2B), but occur at similar heights as defined by faunal changes on a species-height plot (e.g., Fig. 2A). There is a significant faunal change between spindle-dominated lower levels and frond-dominated intermediate levels at 6–8 cm on the D and E surfaces. This shift is marked by the transition between ostrich feathers and *Charniodiscus* on the Lower Mistaken Point surface, also at ~8 cm height. The intermediate level fauna is replaced abruptly at 22 cm on all surfaces with a monospecific upper suite of tall fronds (either *Charnia* or *Charniodiscus*). Subdivisions within this 8–22 cm range can be complex, as on the E surface, or simply partitioned between a lower and up-

per taxon, as seen in the division between pectinates and *Bradgatia* on the D surface. Extremely tall specimens are also present on the Lower Mistaken Point surface, suggesting that there may be another suite of taxa that dominates heights exceeding 1 m. A composite diorama of tiered Mistaken Point communities is given in Figure 3.

Ediacaran tier boundaries (6–8 cm, 22 cm, 35 cm, and possibly ~100 cm) are similar to the levels recognized by Bottjer and Ausich (1986) for Phanerozoic communities of skeletal organisms (5 cm, 20 cm, 50 cm, and 100 cm). The only significant difference occurs in the upper boundary of the third tier (35 cm versus 50 cm); however, the rarity of preserved specimens >35 cm at Mistaken Point obscures the exact tier boundary. The maximum height in tiered Ediacaran communities (~90–120 cm) is the same as the upper size limit in Paleozoic skeletal communities (Bottjer and Ausich, 1986). In addition, the dominance of small (<10 cm tall) specimens is consistent with Phanerozoic population size distributions (Watkins, 1991; Taylor and Brett, 1996). In contrast to Phanerozoic communities, infaunal tiering is not developed in Ediacaran communities, and definite burrows are absent from Mistaken Point.

DEEP-WATER VERSUS SHALLOW-WATER COMMUNITIES

Bottjer and Ausich (1986) explicitly addressed tiering only in shallow-water communities, because deep-water organisms tend to be taller to compensate for slower bottom

currents and a thicker boundary layer. Comparison of recorded fossil heights from shallow-water Ediacaran localities (cf. Ausich and Bottjer, 2001) provides an indication that the tiering structure of Mistaken Point communities may be representative of Ediacaran communities in general. For example, lower levels in Australian communities may have included *Tribrachidium* and *Arkurua*, with frondose taxa to 73 cm in height occupying intermediate and upper levels (Jenkins and Gehling, 1978; Jenkins, 1992; Ausich and Bottjer, 2001). Similarly, lower feeding levels in Namibia were dominated by *Beltanelliformis*, *Ernietta*, and small fronds (e.g., *Rangea*); larger fronds (e.g., *Swartpuntia*) to 25 cm in length were also present (Jenkins, 1992; Narbonne et al., 1997). These published measurements suggest that the tiering at Mistaken Point was comparable to that of shallow-water Ediacaran communities and was not merely a response to deep-water hydrodynamic conditions.

TIER COMPOSITION

Although the height of tier boundaries appears relatively consistent between communities, the individual tier constituents display a considerable amount of plasticity. Most organisms may occur in different tiers at different sites or in multiple tiers at a single site. For example, *Charnia* is characteristic of the upper level on the D surface, but occurs mainly at intermediate heights in the E surface community, and is found at all heights at Lower Mistaken Point, dominating at heights where more specialized tierers at that locality were not present. The fact that tier composition varies significantly between communities suggests that some organisms were filling the same ecological niche and could occupy different tiers interchangeably, depending on their population structure (governed by chance factors such as time of recruitment). Only spindles are invariably confined to a single tier (lowest level), likely for constructional reasons. Spindles allocate most of their biomass in horizontal growth, whereas all other organisms are dominantly upward growing, so that even the oldest and largest spindles would be shorter than most frondose taxa.

EDIACARAN FEEDING STRATEGIES

Various feeding strategies have been proposed for Ediacaran taxa, including photosynthetic or photosymbiotic (McMenamin, 1986), absorbing dissolved nutrients directly from seawater (Seilacher, 1989), and suspension feeding (Jenkins and Gehling, 1978). Photoautotrophic methods can be discounted for Mistaken Point communities because the organisms were living in deep water well below the photic zone (Seilacher, 1992; Narbonne et al., 2001); however, both absorption of dissolved matter and filter feeding are consistent

with the development of a tiered epifaunal structure. In both cases nutrients are derived from horizontally flowing bottom currents, favoring epifaunal tiering to increase feeding efficiency by partitioning nutrient supplies.

Analogues of colonial tierers and solitary tierers (Bottjer and Ausich, 1986) are also found in the Ediacaran ecosystems at Mistaken Point. Although it is not possible to determine whether Ediacaran organisms were colonial or solitary, they have adopted the same feeding strategies as Phanerozoic colonial and solitary tierers. Ediacaran organisms such as *Bradgatia*, *Charnia*, and spindles collected nutrients along their entire length, exploiting a similar strategy to Phanerozoic colonial corals and bryozoans. However, *Charniodiscus*, dusters, and ostrich feathers were more similar to Phanerozoic crinoids in having a specialized frond suspended above the seafloor. Both of these feeding strategies are also well represented in shallow-water Ediacaran ecosystems in Australia, Namibia, and the White Sea.

CONCLUSIONS

Epifaunal tiering is well developed in Ediacaran communities at Mistaken Point. Data from three fossil surfaces show that biomass is concentrated in the basal 10 cm above the seafloor, and abundance declines exponentially with height to a typical maximum of 30–35 cm, with some fronds as tall as 1 m. Absolute boundaries between levels are relatively consistent between assemblages, but the faunal composition is quite variable. Tiering structure in these Ediacaran communities appears to have been controlled by both constructional differences between taxa and chance factors such as age structure and order of colonization. The primary subdivision of Phanerozoic suspension feeders, between organisms and/or colonies that feed along their entire length and ones that suspend their feeding apparatus above the seafloor, is also evident in these Ediacaran communities. The affinities of the Ediacara biota are uncertain, but the tiering structure in Ediacaran communities is strikingly similar to that of Phanerozoic suspension-feeding animal communities.

This study shows that complex epifaunal tiering first evolved in soft-bodied communities, predating development in skeletal assemblages by more than 50 m.y. The apparent tiering reduction across the Precambrian-Cambrian boundary (cf. Ausich and Bottjer, 2001) may be a preservational artifact, but alternatively may have resulted from late Precambrian extinctions of Ediacara taxa and/or cropping of upper tier organisms by evolving Cambrian macropredators. Although there are no organisms in common between Mistaken Point communities and Phanerozoic skeletal assemblages, many key properties of tiered Phanerozoic ecosystems—such as approximate tier boundaries, maximum organism height, and dominance of low-level organisms—were initiated in soft-bodied communities in the late Neoproterozoic.

REFERENCES CITED

Anderson, M.M., and Misra, S.B., 1968, Fossils found in the Precambrian Conception Group in southeastern Newfoundland: Nature, v. 220, p. 680–681.

Ausich, W.I., and Bottjer, D.J., 1982, Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic: Science, v. 216, p. 173–174.

Ausich, W.I., and Bottjer, D.J., 2001, Sessile invertebrates, *in* Briggs, D.E.G., and Crowther, P.R., eds., Palaeobiology II: Oxford, Blackwell Science, p. 384–386.

Bottjer, D.J., and Ausich, W.I., 1986, Phanerozoic development of tiering in soft substrata suspension-feeding communities: Paleobiology, v. 12, p. 400–420.

Brett, C.E., and Liddell, W.D., 1978, Preservation and paleoecology of a Middle Ordovician hardground community: Paleobiology, v. 4, p. 329–348.

Buss, L.W., and Seilacher, A., 1994, The phylum Vendobionta: A sister group of the Eumetazoa?: Paleobiology, v. 20, p. 1–4.

Cannell, M.G.R., and Grace, J., 1993, Competition for light: Detection, measurement, and quantification: Canadian Journal of Forestry Research, v. 23, p. 1969–1979.

Chen, J., and Zhou, G., 1997, Biology of the Chengjiang fauna, *in* Chen, J., et al., eds., The Cambrian explosion and the fossil record: National Museum of Natural Science Bulletin, v. 10, p. 11–106.

Conway Morris, S., 1986, The community structure of the Middle Cambrian Phyllopod Bed (Burgess Shale): Palaeontology, v. 29, p. 423–468.

Conway Morris, S., 1993, Ediacaran-like fossils in Cambrian Burgess Shale–type faunas of North America: Palaeontology, v. 36, p. 593–636.

Foster, M.J., 1975, Algal succession in a *Macrocys-tis pyrifera* forest: Marine Biology, v. 32, p. 313–329.

Jenkins, R.J.F., 1992, Functional and ecological aspects of Ediacaran assemblages, *in* Lipps, J.H., and Signor, P.W., eds., Origin and early evolution of the Metazoa: New York, Plenum, p. 131–176.

Jenkins, R.J.F., and Gehling, J.G., 1978, A review of the frond-like fossils of the Ediacara assemblage: South Australian Museum Records, v. 17, p. 347–359.

Landing, E., Narbonne, G.M., and Myrow, P., 1988, Trace fossils, small shelly fossils and the Precambrian-Cambrian boundary: New York State Museum and Geological Survey Bulletin, v. 463, 81 p.

Lane, N.G., 1963, The Berkeley crinoid collection from Crawfordsville, Indiana: Journal of Paleontology, v. 37, p. 1001–1008.

McMenamin, M.A.S., 1986, The garden of Ediacara: Palaios, v. 1, p. 178–182.

Misra, S.B., 1971, Stratigraphy and depositional history of late Precambrian coelenterate-bearing rocks, southeastern Newfoundland: Geological Society of America Bulletin, v. 82, p. 979–988.

Myrow, P.M., 1995, Neoproterozoic rocks of the Newfoundland Avalon zone: Precambrian Research, v. 73, p. 123–136.

Okada, H., and Ohta, S., 1993, Photographic evidence of variable bottom-current activity in the Suruga and Sagami bays, central Japan: Sedimentary Geology, v. 82, p. 221–237.

Narbonne, G.M., 1998, The Ediacara biota: A terminal Neoproterozoic experiment in the evolution of life: GSA Today, v. 8, p. 1–6.

Narbonne, G.M., Saylor, B.Z., and Grotzinger, J.P., 1997, The youngest Ediacaran fossils from southern Africa: Journal of Paleontology, v. 71, p. 953–967.

Narbonne, G.M., Dalrymple, R.W., and Gehling, J.G., 2001, Neoproterozoic fossils and environments of the Avalon Peninsula, Newfoundland. Geological Association of Canada Annual Meeting, Field Trip Guidebook B5: St. John's, Geological Association of Canada, 100 p.

Runnegar, B., 1995, Vendobionta or Metazoa? Developments in understanding the Ediacara "fauna": Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 195, p. 303–318.

Seilacher, A., 1989, Vendozoa: Organismic construction in the Proterozoic biosphere: Lethaia, v. 22, p. 229–239.

Seilacher, A., 1992, Vendobionta and Psammocorallia: Lost constructions of Precambrian evolution: Geological Society of London Journal, v. 149, p. 607–613.

Seilacher, A., 1999, Biomat-related lifestyles in the Precambrian: Palaios, v. 14, p. 86–93.

Taylor, W.L., and Brett, C.E., 1996, Taphonomy and paleoecology of Echinoderm *Lagerstätten* from the Silurian (Wenlockian) Rochester Shale: Palaios, v. 11, p. 118–140.

Watkins, R., 1991, Guild structure and tiering in a high-density Silurian community, Milwaukee County, Wisconsin: Palaios, v. 6, p. 465–478.