LETTERS

My compliments to Bottjer et al. (2000) for their thoughtful and stimulating discussion of changes in level-bottom fossil communities near the Proterozoic-Cambrian transition! However, in addition to the changes on or in siliciclastic substrates enumerated by them, there was another contemporaneous substrate revolution involving: (a) increased diversity of reef-building taxa; part of the well-documented "Cambrian explosion" of skeletal metazoans; and (b) a switch in growth habit and/or direction and growth forms and/or shapes among reef-building taxa from mostly subhorizontal, microbial mats or sheets (stromatolites) to densely packed skeletal tubules *(Epiphyton)*, coccoids *(Renalcis)* and erect cups or bowls and sticklike cylinders or cones of the early Archaeocyatha.

In contrast to the frameless Precambrian reefs built exclusively by soft-bodied microbes, the Cambrian reef revolution produced the earliest reefs with skeletal frameworks (Kruse et al., 1995). The nearly simultaneous appearance of weakly skeletonized *Epiphyton, Renalcis* (both calcimicrobes), and Archaeocyatha (Porifera) characterized the abundant and diverse Early Cambrian fossil reef communities.

Furthermore, the nearly coincident increase in packing density of calcimicrobes and clonal Archaeocyatha provided sufficient skeletal volume and rigidity to build the initial self-supporting reef framework. Accompanying this truly revolutionary increase in morphologic diversity, skeletonization, packing density and erect clonal growth, there also was a progressive increase in the complexity of reef guild structures from the Precambrian through the Early Cambrian (Fagerstrom, 1986, p. 325–331).

In summary, the Cambrian substrate experienced revolutions on or in siliciclastic detrital sediments as well as in the building of small, topographically elevated carbonate reefs with skeletal frameworks. The appearance of skeletal reef substrates was at least as profound as the revolution described by Bottjer et al. (2000).

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Bottjer et al. reply: In our paper we outlined the changes in seafloor character that occurred due to the evolution of increasing vertically directed bioturbation. Thus, shallow seafloors in the late Neoproterozoic which had been microbial mat-dominated were largely replaced in the Cambrian and post-Cambrian by seafloors with a surface mixed layer, a change that has been called the agronomic revolution. This change in benthic substrates strongly impacted metazoans adapted to mat-dominated seafloors and yielded profound long-term evolutionary and ecological effects that we have termed the Cambrian substrate revolution.

Fagerstrom has aptly summarized contemporaneous changes that were occurring in carbonate buildups. These were largely due to changes in microbial communities and inclusion of skeletal metazoans. Yet, still more work is needed to understand the response by early metazoans to the change from substrates largely physically structured by microbial mat-forming communities to those altered by the activity of other metazoans. For example, the earliest crustaceans are hypothesized to have evolved in the late Neoproterozoic and were likely relatively small (Walossek, 1999). Thus, one can ask, How did interacting with a seafloor structured by microbial mats affect the early evolution of the Crustacea, and how did they later respond as part of the Cambrian substrate revolution? Where appropriate, similar questions must be asked of other early metazoan clades.

Until recently we had only begun to scratch the surface on understanding the evolutionary and environmental context for the early evolution of metazoans. However, a variety of pieces of the puzzle are falling into place, making this one of the most exciting fields of inquiry in geobiology today.

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