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## **Foraminifera living in sulfidic environments: Biology, ecology, and geological implications**

Joan M. Bernhard

*Woods Hole Oceanographic Institution, MS 52, Department of Geology & Geophysics,  
Woods Hole, MA 02543, U.S.A. jbernhard@whoi.edu*

Foraminifera are considered to be aerobes but observations from the past two decades suggest that at least some species are facultative anaerobes capable of surviving considerable periods of anoxia (i.e., lack of dissolved oxygen) and sulfide enrichment (e.g., exceeding 10  $\mu\text{M}$ ). An overview will be presented of the cell ultrastructure and ecology of these potentially anaerobic, sulfide-tolerant benthic foraminifers, which occur in sediments of silled basins, gas seeps, and fjords. The observed cell biological strategies that these foraminifers have employed to survive these seemingly “extreme” environments include presence of endosymbionts or ectosymbionts, sequestration of functional chloroplasts, and proliferation of peroxisomes and endoplasmic reticulum. Commonly, distributions of foraminiferal mitochondria are unusually structured (e.g., at cell periphery, in dense groupings within the cell, or associated with endoplasmic reticulum). Interestingly, species of both calcareous and agglutinated foraminifers are known to have prokaryotic (non-photosynthetic) symbionts.

Distributional studies indicate that some species are more abundant in sulfide-enriched sediments than in oxygenated sediments. Ecological methods using a fluorescently-labeled embedded core technique to preserve, on the micron-scale, the positions of live individuals in sediments establish that some foraminiferal taxa live well within euxinic sediments. It is important to note, however, that some specimens, which were collected from seeps and stain with Rose Bengal, lack any intact organelles. These well-stained seep specimens, thus, were dead at the time of collection.

Observations have various implications for the interpretation of the geologic record. For example, data suggest that while the  $\text{d}^{13}\text{C}$  signatures of cold-seep foraminiferal calcite may indicate presence of authigenic carbonate overgrowths, it is also possible that foraminifera that actually live in active seeps precipitate calcite with a signature at least partly influenced by the chemistry of the seep emanations. From a different perspective, collective observations support the possibility that non-calcareous symbiont-bearing foraminifers were pivotal players in benthic-ecosystem structuring of

Proterozoic sulfidic, oxygen-depleted oceanic sediments, and that, due to their bacterial endobionts, they furthermore played a significant role in biogeochemical processes during that period of dramatic global oceanic and atmospheric change. Findings warrant a re-examination of the Proterozoic stratigraphic record, which should include a new microfossil-search pattern focusing on thin-shelled, fine-grained allogromiid foraminiferal remains.