

Evolution and the Fossil Record, B. Runnegar, J. W. Schopf, Eds. (Paleontological Society Short Courses in Paleontology, Paleontological Society, Pittsburgh, PA, 1988), pp. 114–129; in *Early Life on Earth*, S. Bengtson, Ed. (Columbia Univ. Press, New York, 1994), pp. 36–47.

2. The loss of ammonia in the Early Archean should have taken place by photochemical destruction as well as by oxidative loss, both processes placing evolutionary pressure on all forms of life to evolve some way of obtaining this important material.

Response

TOWE ARGUES THAT AN ENERGETICALLY expensive enzyme such as nitrogenase would not have evolved in the early environment of the Archean oceans where reduced forms of nitrogen were available, and that the impetus for nitrogenase evolution coincided with the oxygenation of the atmosphere (by cyanobacteria) and loss of ammonia via oxidation.

The availability of fixed forms of nitrogen would certainly have influenced the evolution of biological fixation of nitrogen and of the enzyme responsible, nitrogenase. Evidence demonstrates that nitrogenase is a highly conserved enzyme in eubacteria and cyanobacteria, with phylogenetic analyses clearly suggesting a single ancestral origin for the catalytic subunits of the enzyme complex (1) that preceded the oxygenation

of the atmosphere and the oxidative destruction of ammonia (NH_3). The presence of nitrogen-fixing organisms as early as 3.3 billion years ago implies that reduced nitrogen would have already been scarce. Indeed, current models propose that CH_4 and not CO_2 warmed the planet, thereby limiting NO formation from N_2 and CO_2 (2). Additionally, ultraviolet radiation would cause rapid dissociation of NH_3 in the atmosphere with little fallout to the oceans (2, 3).

Furthermore, the nitrogenase complex is nonspecific and reduces triple-bond molecules such as hydrogen azide, nitrous oxide, acetylene, and hydrogen cyanide. Primitive forms of nitrogenase might have evolved as a N_2 respiratory enzyme (N_2 being an accessible electron sink for anaerobic heterotrophs under the reducing conditions) or as a detoxase that would have detoxified cyanides and other prevalent molecules in the ancient oceans (4, 5). With the loss of free ammonia and cyanides, nitrogenase would have evolved to become the prevalent biological mechanism for nitrogen acquisition before the oxygenation of the atmosphere and the advent of nitrification (3, 5).

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References and Notes

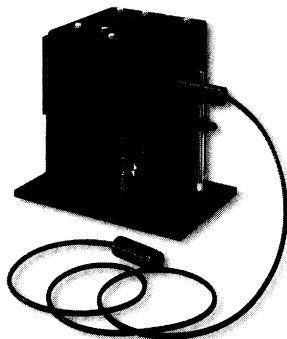
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CORRECTIONS AND CLARIFICATIONS

LETTERS: "Minimizing effects of CO_2 storage in oceans" by G. H. Rau, K. Caldeira (11 Jan., p. 275). The amount of carbon ingested and stored by the oceans each year was mistakenly edited to read ~2 picograms per year instead of ~2 petagrams.

LETTERS: "Etymology of epigenetics," letter by H. Rubin, response by C.-t. Wu (21 Dec., p. 2477). Misinterpretation of the response during the editing process led to an erroneous statement in note 4, which implies that C. H. Waddington discussed "epigenetics" in his 1939 book *An Introduction to Modern Genetics*; Waddington only alluded to the concept, leaving his formal definition of "epigenetics" to later.

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