OXYGEN AND THE EVOLUTION OF THERMOACIDOPHILES.

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Introduction: One of the outstanding challenges in astrobiology is to understand the feedbacks between microbial and geologic processes through Earth history. The activities of microorganisms influence the chemistry of their local environment, which in turn shapes the ecological and evolutionary drivers that promote their diversification in a process described as niche construction [1]. Volcanic ecosystems continue to be an area of key focus in habitability research since they represent the upper temperature and lower pH bounds of habitable niche space. In particular, acidic environments have served as model platforms for understanding the interactions between microorganisms and their geologic settings in both contemporary and deep-time contexts [2-4]. However, little is known of how these environments and the organisms that inhabit them have evolved. Here, we provide evidence that hyperacidic (pH < 3.0) hydrothermal ecosystems are dominated by a limited number of archaeal lineages that exhibit a near universal ability to use oxygen (O_2) in high energy-yielding respiratory metabolisms, are recently evolved, and are responsible, in part, for the formation of hyperacidic hydrothermal environments. We further hypothesize that neither these lineages nor acidic hydrothermal environments were widespread until the recent geologic past.

Geochemical Context: Yellowstone National Park (YNP) hot springs vary in their geochemical composition and include an abundance of acidic springs (pH < 3.0). The oxidation of sulfur compounds is responsibe for the acidification of these environments and these processes have a significant biotic component [2,5-6] that is dependent on aerobic thermoacidophiles. We characterized the diversity, distribution and physiological characteristics of microbial populations inhabiting 72 representative hot spring environments in YNP that span a pH range of 2.1 to 9.6 and a temperature range of 32.7 to 92.5°C.

Molecular Microbial Data: Analysis of 16S rRNA gene abundances revealed a transition toward aerobic archaeal dominance of acidic springs. Phylogenomic analyses of 584 publically available archaeal genomes revealed that acidophily evolved independently multiple times within the Archaea, each coincident with the emergence of the ability to integrate O_2 into their energy metabolism, and that these events likely occurred in their recent evolutionary past. The genomes of archaeal thermoacidophiles are also enriched in similar protein-coding genes, consistent with convergent evolution aided by horizontal gene transfer. The culmination of these results indicate a central role for O_2 in the co-evolution of acidophilic taxa and hyperacidic environments through the little studied process of niche construction [1]. In this process, the biological production of acidity resulted in the development of high-temperature acidic niche-space that promoted the radiation of aerobic organisms responsible for acidification, and their respective lineages.

Conclusions: Based on empirical O_2 tolerance thresholds, we suggest that dissolved O_2 concentrations in thermal waters likely did not reach levels capable of sustaining aerobic thermoacidophilic Archaea and their acidifying activity until O_2 levels reached present atmospheric levels ~0.8 Gya [7]. Because the development of acidic environments and their successful habitation both require O_2 [2,5,6], these results indicate that thermoacidophilic Archaea and the acidity of their habitats co-evolved after the evolution of oxygenic photosynthesis. These results provide new insight into the role of biology in the expansion of Earth's habitable niche-space (acidic environments), which may be an example of how planetary habitability can be enhanced through biological activity which, in turn, further promotes the diversification of life.

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