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## Precipitation of greigite and pyrite induced by Thermococcales: an advantage to live in Fe- and S-rich environments?

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1 *Precipitation of greigite and pyrite by Thermococcales: Ensuring survival in Fe- and S-rich*  
2 *environments*

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23  
24  
25 **Abstract**

26

27 Hydrothermal deep-sea vents, one of the most extreme environments for life on Earth, are  
28 iron- and sulfur-rich anaerobic systems. Whereas FeS<sub>2</sub> pyrite is abiotically formed in the  
29 interior of active sulfide chimneys at high temperatures (> 250°C), a major stock of FeS<sub>2</sub>  
30 pyrite is also produced in the cooler middle layers of the chimneys at lower temperatures (<  
31 150°C) by a still unknown mechanism. *Thermococcales*, a major family of archaea inhabiting  
32 these extreme environments, have been shown to rapidly produce abundant quantities of FeS<sub>2</sub>  
33 from the hydrothermal fluid at 85°C, suggesting that they may contribute to the formation of  
34 “low temperature” FeS<sub>2</sub> pyrite in their ecosystem. In this study, we show that this mechanism,  
35 which induces a massive cell mortality, operates in *Thermococcus kodakarensis* only when  
36 zero-valent sulfur is directly available as sulfur vesicles. Significant amounts of Fe<sub>3</sub>S<sub>4</sub> greigite  
37 nanocrystals are then formed extracellularly nucleating on iron-phosphate-bearing  
38 extracellular materials presumably resulting from cell lysis. Those pyrite and greigite  
39 mineralizations allow the formation of a 3D structure composed of pyrite-mineralized cells  
40 and vesicles remnants within a matrix consisting mostly of greigite nanocrystals. Starting  
41 from this state, we observe that a new generation of cells grew in this medium a priori not  
42 adapted to cell growth. We propose that greigite precipitation on phosphate-loaded former cell  
43 materials induces the release of phosphates and organic compounds thus making them  
44 available to a few surviving non-mineralized cells hence allowing production of new alive  
45 cells. This suggests that biologically induced iron-sulfides mineralization could be part of a  
46 survival strategy employed by *Thermococcales* to cope in strongly mineralizing high-  
47 temperature hydrothermal environments.

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49 **Keywords**

50 Biomineralization, Pyrite, Greigite, Hyperthermophiles, *Thermococcales*, Adaptation

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