LETTER

Reply to Dvořák et al.: Apparent evolutionary stasis of ancient subseafloor sulfur cycling biocoenoses

We thank Dvořák et al. for their comment (1) on our paper (2), in which we compare sulfur-cycling ∼1.8- and ∼2.3-Ga fossil communities with their modern counterparts and report that the community fabric of the fossil and modern microbes, as well as their organismal and cellular morphology, their interlinked energy-production via anaerobic sulfate-reduction and sulfur species oxidation, and their use of sulfate and nitrate to fuel this sulfur cycle appear to have remained unchanged over a segment of geological time equivalent to half the age of the Earth. Given these observations, our paper suggests that the apparent long-term stasis of the form, function, and metabolic requirements of this ecosystem may be attributable to the seemingly unchanging physical-biological characteristics of its subseafloor environment, a possible example of evolution's null hypothesis.

Although the Dvořák et al. comment (1) may in part be relevant to our discussion, because the reported extreme polyphyleticism among *Synechococcus*-like cyanobacteria on which it is based has "not been observed in any other cyanobacteria" (3), it is unknown whether this finding in actuality "illustrates general trends in cyanobacterial evolution" (3). Moreover, oxygen-producing phototrophic cyanobacteria, among the most morphologically diverse and distal members of the bacterial phylogenetic tree, are only distantly related to the anaerobic sulfur-cycling bacteria we report (2). Thus, the relevance of cyanobacterial evolution to that of such colorless sulfur bacteria is open to question and the conjecture by Dvořák et al. that the polyphyleticism inferred for *Synechococcus*-like cyanobacteria may be applicable "more broadly [to all] prokaryotic evolution" (3) is unsubstantiated, as are the age and source of the biomarkers (4, 5) used by Dvořák et al. to calibrate their cyanobacterial chronograms (3). On such bases, Dvořák et al. suggest that the stasis of the sulfur-cycling communities "might be explained by serial convergence of phenotypic traits, which masks possible continuous metabolic, genetic, and ecological changes" (1). As we discuss in our paper, however, ecosystem-altering changes in metabolism and ecology seem contraindicated by the available evidence, whereas genotypic changes can be inferred in fossils only from changes in phenotype that for the fossil and modern bacteria seem essentially identical (2).

The potentially most relevant aspect of the Dvořák et al. comment (1) is their note that convergence has been reported for "giant" microaerophilic or aerobic sulfur bacteria, such as *Beggiatoa* and *Thioploca*, a matter addressed in our paper in which we point out that such bacteria are not present in the fossil communities and that convergence has not been reported for any of the several morphotypes of <10-μm-diameter anaerobic sulfur-cycling bacteria we describe (2).

We regard it likely that additional subseafloor anaerobic sulfur-cycling communities will be discovered to fill the gap between the mid-Precambrian and the present and that these will be fundamentally similar in their form, function, and metabolic requirements to those described in our paper, but we note also that firm acceptance of our preferred explanation for the hypobradytelic stasis of this ecosystem would at present be premature (2).

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1 Dvořák P, Casamatta DA, Hašler P, Poulíčková A (2015) Putative extremely long evolutionary stasis in bacteria might be explained by serial convergence. *Proc Natl Acad Sci USA* 112:E2559.
2 Schopf JW, et al. (2015) Sulfur-cycling fossil bacteria from the 1.8-Ga Duck Creek Formation provide promising evidence of evolution's null hypothesis. *Proc Natl Acad Sci USA* 112(7): 2087–2092.
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4 French KL, et al. (2013) Archean hydrocarbon biomarkers: Archean or not? *Mineral Mag* 77(5):1110 (abstr).
5 Hoshino Y, Flannery DT, Walter MR, George SC (2015) Hydrocarbons preserved in a ∼2.7 Ga outcrop sample from the Fortescue Group, Pilbara Craton, Western Australia. *Geobiology* 13(2):99–111.

Author contributions: J.W.S., A.B.K., M.R.W., M.J.V.K., K.H.W., R.K., J.W.V., V.A.G., C.E., and D.T.F. wrote the paper.

The authors declare no conflict of interest.

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www.pnas.org/cgi/doi/10.1073/pnas.1503754112