

REPLY TO WANG AND CHEN:

An ancient origin of magnetotactic bacteria

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Our recent paper (1) reports an ancient origin of magnetotactic bacteria (MTB) before or near the divergence between the phyla *Nitrospirae* and *Proteobacteria*, which has implications for the Archean geomagnetic field and paleoenvironment.

Wang and Chen (2) appear to have misunderstood our paper, noting that we only consider the inference of a magnetotactic ancestor of *Proteobacteria* and *Nitrospirae*. However, this is only one of the suggestions in our paper. We do not rule out the possibility of undetected ancient horizontal gene transfer (HGT) between these phyla and clearly mention in our paper that magnetosome gene clusters (MGCs) were “present before the separation of the *Nitrospirae* and *Proteobacteria* phyla, or transferred undetectably early between the base of *Nitrospirae* and *Proteobacteria* soon after divergence.”

Wang and Chen also raise questions about the high loss rate of MGCs. First, their analysis of 16S rRNA genes (figure 1 in ref. 2) is missing many MTB sequences, for example, *Nitrospirae* (3), *Deltaproteobacteria* (4, 5), and *Gammaproteobacteria* (6), making their assessment of loss rate inaccurate. Second, the metabolic/bioenergetic cost of replicating MGCs and forming magnetosomes is high (7). When the magnetotactic advantage is small or zero with respect to its energy cost, it is energetically favorable to no longer produce magnetosomes. As a consequence, the frequency of spontaneous loss of magnetosome genes in cultivated MTB is known to be high (8). Such a high loss over short laboratory timescales could translate to a significant loss rate of geological times. Third, MTB occupy a specific environmental niche, requiring environmental gradients and a magnetic field.

Putting natural MTB populations in a zero field drives some MTB populations down (9). It is therefore not surprising that MTB are sensitive to unfavorable environments and can be outcompeted by other microorganisms. A high loss rate of the MGCs throughout bacterial lineages should be expected.

Wang and Chen also suggest that our analysis against recent HGT is unconvincing due to a perceived small number of MTB and the likely saturation of substitution rate per synonymous site (dS). For our study, we have included all available genomes of MTB in *Proteobacteria* and *Nitrospirae* (12 genomes as of January 2016), which to our knowledge is the most comprehensive genomic analysis of MTB ever undertaken. The dS values in our study are all <2, which are considered acceptable by modern standards (10). Furthermore, we use a combination of phylogenetic congruence, codon use bias, dS, and sequence homology-based analyses to robustly rule out recent HGTs between these phyla.

Finally, Wang and Chen raise a hypothesis that MGCs originated in *Alphaproteobacteria* and were transferred to some members of *Nitrospirae* and *Deltaproteobacteria* through ancient HGT. However, they do not provide any evidence to support this. Although their cited references hypothesize ancient transfer between *Nitrospirae* and *Proteobacteria*, a scenario that we consider in our paper, none of these references has suggested the origin of MGC in *Alphaproteobacteria* and transfer specifically from *Alphaproteobacteria* to *Nitrospirae* and *Deltaproteobacteria*. Furthermore, this hypothesis cannot explain the distribution of MTB in *Gammaproteobacteria* and perhaps in other classes of *Proteobacteria*.

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