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PNAS LETTER

Magnetosome proteins belong to universal protein families involved in many cell processes

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Magnetic sensing is a fascinating biological function whose origin in eukaryotes still remains poorly understood, unlike in magnetotactic bacteria (MTB) (1). The hypothesis of ancient symbiotic events leading to the transfer of magnetite biomineralization from MTB to eukaryotes has been raised for decades (2). In our opinion, this parallel has been made prematurely in Bellinger et al. (3) after their discovery of magnetite in salmonid olfactory epithelium. This observation leads the authors to a biased overinterpretation of the transcriptomic data in favor of the conclusion that genes responsible for magnetite biomineralization in bacteria were inherited by the last common eukaryotic ancestor and are conserved across all domains of life. While we do not question the presence of magnetite in salmonid olfactory epithelium, we have serious concerns about the conclusions drawn on its mechanistic basis and evolutionary origin.

Bellinger et al. (3) establish a direct relationship between the function of <2% of the genes differentially expressed in magnetic relative to nonmagnetic olfactory cells and that of a few magnetosome genes. However, there is no evidence supporting that magnetite biomineralization genes claimed

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The authors declare no competing interest.

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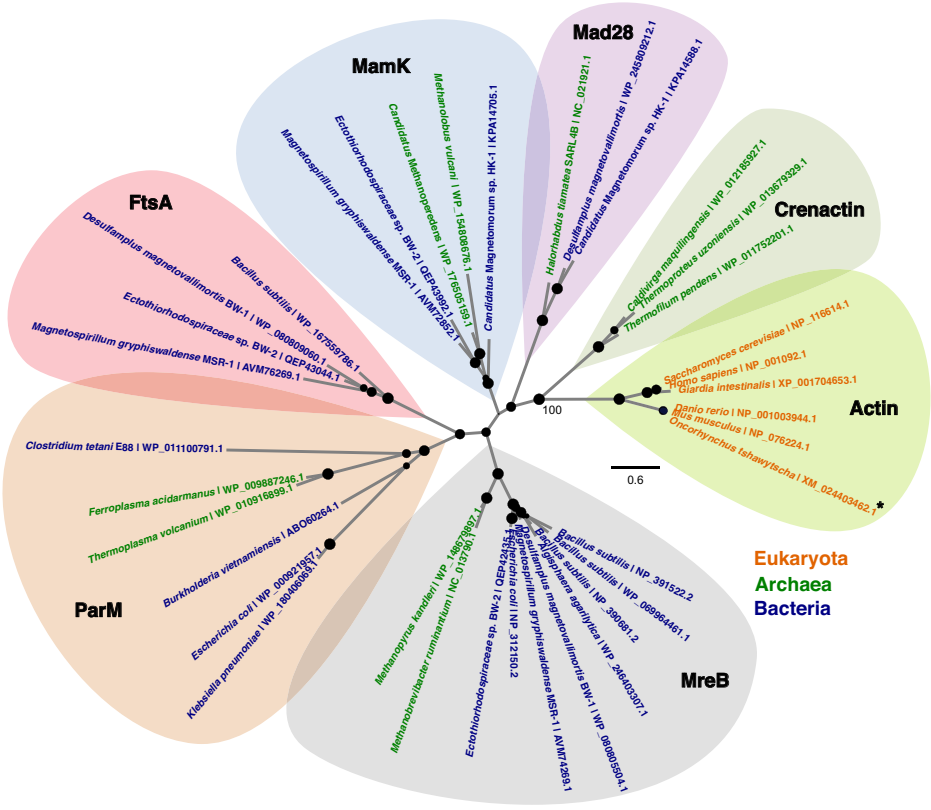


Fig. 1. Unrooted maximum likelihood phylogenetic tree of the actin ATPase protein family showing that the sequence representing the actin-like protein overexpressed in the magnetic olfactory salmon cells (XM_024403462.1; noted "*") clusters with the eukaryotic actin protein family and not with sequences of other actin-related protein families to which belong MreB, Mad28, and MamK encoded in some MTB. The maximum likelihood tree was built using IQTREE version 2.3.0 after substitution model selection on filtered alignments obtained with MAFFT version 7.49. The tree was drawn to scale, and circles represent statistical support estimated from 500 nonparametric bootstraps. The maximum circle size representing a bootstrap value of 100 is annotated on one of the nodes. The sequence database was inspired by that of Ettema et al. (9) and includes a diversity of organisms from all domains of life. Accession numbers are given in the sequence header colored by the domain of life to which the organism belongs.

to be found in the salmon olfactory cells are, per se, functionally equivalent magnetosome genes homologs. Indeed, these relationships were inferred from sequence alignments with low amino acid identity and coverage percentages (often <25% for both). In the absence of additional domain architecture comparisons, molecular phylogenetic analyses, and experimental evidence, these thresholds are not suitable to conclude that salmon and MTB have functional counterparts involved in biomineralization with a common evolutionary origin.

The generic low sequence identity percentages obtained while aligning some salmon proteins and signature magnetosome proteins are not surprising and have been well described for years. Indeed, magnetosome proteins belong to widespread and functionally diverse protein superfamilies, such as TPR proteins, CDF transporters, or HtrA-like serine proteases, and, by consequence, share few domains with proteins that have diverse functions not related to biomineralization (4–7). For example, the magnetobacterial protein MamK belongs to a universal family of actins with an ATPase domain that have diverse roles in cell shape, morphogenesis, or cytoskeleton (8, 9). The six salmon actin-related proteins in *Oncorhynchus tshawytscha* share 22.5 to 24.5% of amino acid identity on only ∼14% of their length with the closest MamK gene sequence of an uncharacterized MTB. Phylogenetics unambiguously supports that these salmon proteins belong to the eukaryotic actin family and not that of MamK (Fig. 1).

We draw similar conclusions for other salmon proteins claimed to be MamA, MamB, or MamEO-Nter proteins and made additional observations that questioned even more Bellinger et al. (3) conclusions: 1) Mandatory genes/motifs for the magnetite biomineralization like the unique magnetochrome motif are absent in the salmon transcriptome (10), and 2) the authors omit to mention that similar homologs like the selected 11 overexpressed genes were also underexpressed. Although we cannot rule out the possibility of a common origin of magnetite biomineralization between MTB and eukaryotes yet, the present data may also be compatible with convergent evolution of a magnetite-based magnetic sensing in the salmonids.

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