2-Methylhopanes in bacteria, the sedimentary archive, and implications for the history of Life

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2-methylhopanes (2-MeHop) are molecular fossils of 2-methylbacteriohopanepolyols (2-MeBHPs), lipids produced by a wide range of bacteria to modify their membrane properties[1]. 2-MeHop are preserved for millions of years and abundant in sediments associated with periods of oceanic anoxia[2]. The fact that a diverse range of bacteria contains the *hpnp*-gene involved in the synthesis of 2-MeBHPs[3] challenged the classical hypothesis that their sedimentary occurrence reflects an expansion of (N_2-fixing) cyanobacteria[2,4]. Thus, the elevated occurrence of 2-MeBHPs during the Phanerozoic is currently unexplained.

Here we use phylogenomic, Bayesian relaxed molecular clock and Bayesian stochastic character mapping analyses from 131 cyanobacteria genomes and show that i) some bacteria that make 2-MeBHP, do not contain the *hpnp*-gene, but a closely related gene-type, ii) the 2-MeBHP-genes are widespread in nitrifying bacteria, and iii) marine (N_2-fixing) cyanobacteria had lost the ability to synthesize 2-MeBHPs by the start of the Phanerozoic. This data is combined with a compilation of novel & existing records of 2-MeHop from across the Phanerozoic that confirms an increased abundance during periods of ocean anoxia. At the same time, earth system modelling indicates an increase in marine nitrification rates during these periods. Based on this combination of organic geochemistry, biogeochemical modelling, and molecular biology, we propose the alternative hypothesis that the elevated sedimentary occurrence of 2-MeHop reflects the expansion of nitrifying bacteria during specific periods of the Phanerozoic.

(**1**) Summons, R. E. & Jahnke, L. L. *Geochim. Cosmochim. Acta* 54, 247-251, (1990). (**2**) Kuypers, M. *et al. Geology* 32, 853-856, (2004). (**3**) Welander, P. V. *et al. Proc. Natl. Acad. Sci. U.S.A.* 107, 8537-8542, (2010). (**4**) Summons, R. E. *et al. Nature* 400, 554-557, (1999).